



Durham E-Theses

Morphological Variation in Wild and Domestic Suids

OWEN, JOSEPH,THOMAS,DAVID

How to cite:

OWEN, JOSEPH,THOMAS,DAVID (2013) *Morphological Variation in Wild and Domestic Suids*, Durham theses, Durham University. Available at Durham E-Theses Online: <http://etheses.dur.ac.uk/6950/>

Use policy

The full-text may be used and/or reproduced, and given to third parties in any format or medium, without prior permission or charge, for personal research or study, educational, or not-for-profit purposes provided that:

- a full bibliographic reference is made to the original source
- a [link](#) is made to the metadata record in Durham E-Theses
- the full-text is not changed in any way

The full-text must not be sold in any format or medium without the formal permission of the copyright holders.

Please consult the [full Durham E-Theses policy](#) for further details.

Morphological Variation in Wild and Domestic Suids

Joseph Thomas David Owen

PhD Thesis
Department of Anthropology
Department of Archaeology
Durham University
2012

Table of Contents

Content	Page Number
Declaration	vi
Statement of Copyright	vi
Acknowledgements	vii
1.1 Introduction	1
1.1.1 Structure of the Thesis	3
1.1.2 Pigs Exploitation	8
1.1.3 The Extreme Relationships between Pigs and People	9
1.1.4 Pigs and Social Status	12
1.2 The Biology of Pigs	13
1.2.1 Current Taxonomy	13
1.2.2 Geography, Ecology and Habitat of the Suids Studied	15
1.2.3 The Evolutionary History of Suids	17
1.2.4 Known Biogeographic variation within <i>Sus scrofa</i>	18
1.2.5 Known constraints on <i>Sus scrofa</i> range	20
1.2.7 Suids and Insularity	21
1.3 Domestication	24
1.3.1 Defining the Process of Domestication	27
1.3.2 Defining what a 'Domestic' Animal is	29
1.3.3 How do Animals Become Domesticated?	32
1.3.4 Domestication Pathways	34
1.3.5 Cultural and Biological processes of domestication	36
1.3.5.1 Cultural processes	36
1.3.5.2 Biological processes	36
1.3.6 Changes seen in Domesticated Animals	39
1.3.7 Wild Progenitors	42
1.3.8 The Domestication of Pigs: When, Where and How Many Times?	42
1.3.9 The Study of Domestication	46
1.3.10 Methods used in the Study of Domestication	46
1.3.11 Methodological Issues	47
1.3.12 Alternative Methodologies	50
Bibliography	56
2 Methodology	67
2.1 Material	67
2.1.1 The Suid Cranium	67
2.1.2 Materials	71
2.1.3 Covariates	73
2.1.4 Ageing Methods	74

2.1.5	Biometrics, and issues associated with them	75
2.2	Methods	77
2.2.1	Geometric Morphometrics	77
2.2.2	Generalised Procrustes Analysis	77
2.2.3	Kendall's shape space and tangent space	79
2.2.4	Size	80
2.2.5	Procrustes distances	80
2.2.6	Visualisation techniques	81
2.2.7	Landmarks	82
2.2.8	Data Collection	84
2.2.9	Landmarks used and explanation for choice	84
2.2.10	Estimating intra-observer error	88
2.2.11	Sexual dimorphism	89
2.2.12	Allometry	91
2.3	Methods of Analysis	92
2.3.1	Principal Components Analysis	92
2.3.2	Canonical Variates Analysis	93
2.3.3	Permutation Tests	95
2.3.4	Discriminant Functions	95
2.3.5	Cross Validation	96
2.3.6	Student's and Hotelling's <i>t</i> -tests	97
2.3.7	ANOVA and MANOVA	98
2.3.8	Regression	99
2.3.9	Cluster Analysis and Neighbour Joining Trees	100
2.3.10	Mode of Evolution	101
	Bibliography	104
	Results Chapters	
3	Manuscript 1:	109
	<i>Resolving genetic and morphological phylogenies within Suidae</i>	
	Abstract	110
	Introduction	111
	Materials and Methods	113
	Results	114
	Discussion	116
	Conclusion	117
	Bibliography	118
4	Manuscript 2:	130
	<i>Pigs in Space: Biogeographic variation in Sus scrofa</i>	
	Abstract	131

	Introduction	132
	Materials	138
	Methods	143
	Results	145
	Discussion	150
	Conclusion	152
	Bibliography	154
5	Manuscript 3	161
	<i>Quantifying cranial shape differences between wild boar and domestic pigs (Sus scrofa) using 3D geometric morphometrics and its application to zooarchaeology</i>	
	Abstract	162
	Introduction	163
	Materials	165
	Methods	166
	Results	168
	Discussion	170
	Conclusion	173
	Bibliography	174
6	Manuscript 4	179
	<i>Domestication and Heterochrony in Sus scrofa</i>	
	Abstract	180
	Introduction	181
	Materials	183
	Methods	184
	Results	185
	Discussion	189
	Conclusion	190
	Bibliography	192
	Supporting Information	
	List of landmarks and Image S1	196
	Table S2	199
7	Conclusion	202
7.1.	Evolutionary relationships in suids	202
7.2	Biogeographic variation in suids	202
7.3	Discrimination between wild and domestic suid morphology	203
7.4	Domestication and Heterochrony in <i>Sus scrofa</i>	204
7.5	Strengths, weaknesses and recommendations for future work	205
	Bibliography	205

List of Figures

Figure #	Content	Page Number
	Introduction	
1	Excerpt from Linnaeus' Systema Naturae	2
2	Hair or clothing pins made from pig fibula	9
3	Distribution of <i>Sus</i> haplotypes	19
4	Representation of the scale of interaction between animals and humans	31
5	Summary of the main types of domestication	35
6	Arrival dates and approximate geographical expansions of defined Early Neolithic cultures	44
7	The introduction, introgression and expansion of pig haplotypes into Europe	45
	Methodology	
8	Depiction of the pig skull	
a	Lateral view	68
b	Basicranium	69
c	Dorsal view	71
9	Map showing distribution of samples	73
10	Pig crania depicting landmark positions	
a	Position of landmarks on the cranium	86
b	Position of landmarks on the basicranium	87
11	PCA showing error assessment	89
	Manuscript 1	
1	Map showing distribution of samples	125
2	Genetic and Morphological NJ trees	125
3	PCA and CVA showing group differences	126
4	Maximum Likelihood estimate of the rate and tempo of evolution in suids and Ancestral node scores of suids	127
	Manuscript 2	
1	Map of samples	158
2	Box plot of centroid sizes	159
3	PCA and CVA of <i>Sus scrofa</i>	160
	Manuscript 3	
1	PCA of wild and domestic pigs	177
2	PCAs of cranial landmark subsets	178
	Manuscript 4	
1	PCA of wild and domestic ontogenetic series	195

List of Tables

Table #	Content	Page Number
	Methodology	
1	Test results for sexual dimorphism	91
	Manuscript 1	
1	List of recognised suid taxa and samples used in the analysis	123
S2	Distance matrix of procrustes distances between taxa in Figure 2b	129
S3	Discriminant function scores	129
	Manuscript 2	
1	List of Samples and Covariates	140
2	Discriminant function results	146
	Manuscript 3	
1	Procrustes distances and discriminant functions	169
2	Cross validation results between domestic breeds	170
	Manuscript 4	
1	Distances between wild and domestic groups for complete crania for all age stages	186
2	Distances between wild and domestic groups for complete crania for different age stages	186
3	Angles between ontogenetic trajectories	187
4	Tests for paedomorphism: distances between different ages stages for wild and domestic pigs	187
5	Distances between wild and domestic pigs for partial crania	188
6	Angles between ontogenetic crania for separate parts of the crania	189

Declaration

All work submitted within this thesis was conducted and written by the author, with the following exceptions. The analysis of the mode of evolution in manuscript 2, which was jointly conducted by the author and Prof. P.David Polly (University of Illinois), and the computation of angles between regression trajectories in manuscript 4, which was collaborative work between the author and Prof. Kieran McNulty (University of Minnesota).

Statement of Copyright

The copyright of this thesis rests with the author. No quotation should be published without the author's prior written consent and information derived from it should be acknowledged.

Acknowledgements

'The time has come,' the Walrus said,
'To talk of many things:
Of shoes - and ships - and sealing wax -
Of cabbages - and kings -
And why the sea is boiling hot -
And whether pigs have wings.'

(Lewis Carroll – 1871)

It is a pleasure to thank the many, many people who made this thesis possible.

It is difficult to overstate my gratitude to my PhD supervisor, Dr. Una Strand Viðarsdóttir. Her constant enthusiasm, inspiration, patient and repeated efforts to clearly (and simply) explain things (especially with regard to grammar) helped to make statistics fun and interesting for me. Throughout my PhD, she has provided encouragement, sound advice, good teaching and good company – both in Durham and away on data collection, with lots of good ideas. I consider it a privilege to have been able to work with her, and look forward to many years of collaboration.

I am indebted to my other supervisors, Prof. Keith Dobney, Dr. Greger Larson and Prof Peter Rowley-Conwy. All three have provided great encouragement and counsel, both inspiring me to pursue an academic career whilst spurring me on to achieve. They have mentored me through my formative academic years, affording me many opportunities for which I am exceedingly grateful.

I would also like to thank my colleagues on the research project, Dr Allowen Evin, Dr Thomas Cucchi and Dr Linus Girdland Flink. Their assistance and advice, especially Allowen with statistics, has helped me enormously throughout the PhD. Their companionship during data collection led to some great experiences which I will always treasure. Also, Helgi Pétur Gunnarsson, husband of Una Strand Viðarsdóttir, thank you for digging me out of numerous statistical dead ends, although he did fail the Vienna rib challenge.

I am indebted to my fellow students and good friends for providing such a stimulating and fun atmosphere in which to work and play. Kimberly Plomp and Charlotte ‘Charlie’ King, ably assisted by Dr. Ross Barnett, they created a unique lab environment which I will sorely miss. It’s been a pleasure to explore GMM with you guys and I hope that we will always remain in contact wherever we all end up.

I could not write these acknowledgements without mentioning the roles played by my close friends. Dr Anna Linderholm, whose subtle promptings, firm opinions and sound advice made possible the completion of this thesis. Dr Mike Church also played a large role, helping me over the course of my PhD with his less subtle promptings but equally good advice. Dr Michelle Munde, who I first met in 2002 at the beginning of my undergraduate degree in Durham, has always been there, providing emotional support, camaraderie and entertainment. Thank you all so much.

To all my family; my parents - Shelia and Richard, my Nan, my brothers Nat and Tim and his wife Angie, my sister Rachel and her husband Chris; my parents-in-law Robert and Shelia and my sister in law Jessica. All of you have always encouraged me to pursue my dreams; you have provided me with a loving environment in which to live, I love you all, and thank you.

Finally, to the constant refrain of ‘just get it done’ - there, it is done, finished. If I have forgotten anyone, know that it is because of my shoddy memory, not because I don’t value you or your contributions, so thank you too.

Finally, finally, but most importantly, my wife - Alison Jane Danforth. There is no way that this PhD would have been finished without you. Your love and support has carried me where I would have stumbled. Thank you for putting up with the PhD fog and fury, for all the little things and all the big things. I love you, and this thesis is dedicated to you.

Morphological Variation in Wild and Domestic Suids

1.1 Introduction

Pigs occupy a special place in the human psyche. They are kept both as stock domesticates, like cattle and sheep, and they are treated as companions and aids, like cats and dogs. There are currently nearly two billion (c.1,984,607,000) domesticated pigs in the world kept as stock animals bred for slaughter (Foreign Agricultural Service (FAS), 2012). Keeping pigs as pets has become increasingly popular in western society in recent years and commensalism with pigs is a long-held tradition in Island South East Asia (McDonald-Brown, 2009). Pigs are a key economic resource; however, they are also an animal that inspires strong emotions of attachment or revulsion; seen as loyal, intelligent, courageous and resourceful or unclean, licentious, gluttonous and ignorant (Albarella et al., 2007, Phillips, 2007). As such pigs and pig products are extensively referenced in classical literature and modern pop culture; examples include George Orwell's *Animal Farm*, Circe, a minor Greek goddess who transforms Odysseus' men into pigs when they feast at her table in Homer's *Odyssey*; the warthog Pumba from the movie *The Lion King*, Miss Piggy from *The Muppets* and Spiderpig in the *Simpsons*; pigs continued popularity is a testament to their enduring importance.

As a result of this unique dual positions of pet and produce, pigs have been intensively studied both as domestic and wild animals. The earliest studies of domestic pigs, their form and origins, come from Charles Darwin (1868) and Ludwig Rutimeyer (1860, 1864), whilst the first scientific description of wild *Sus* was by Karl Linnaeus (1740, 1758) (see figure 1).

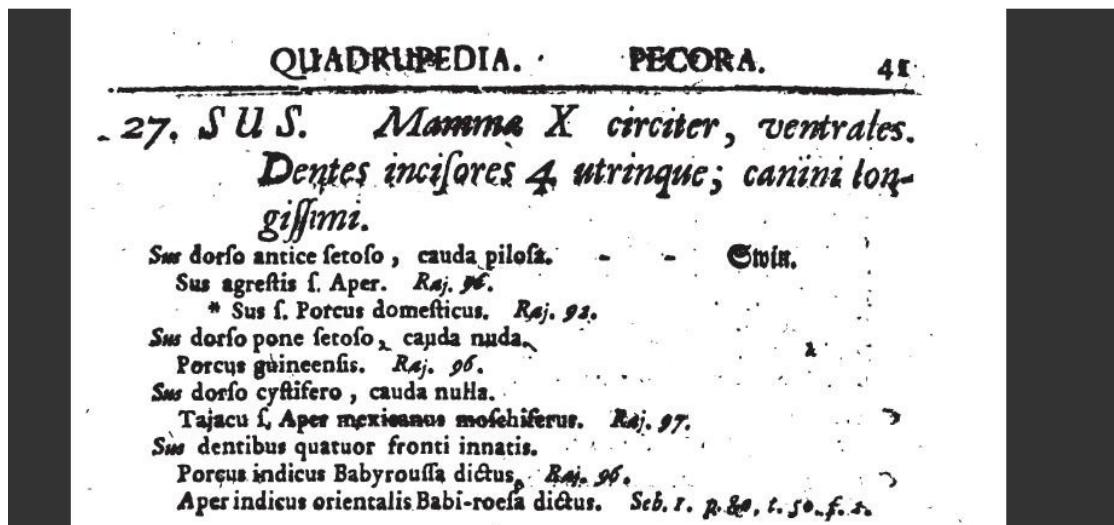


Figure 1: Excerpt from Linnaeus Systema Naturae (1740: second edition)

Here I continue the investigation of the pig, particularly the evolution of wild and domestic pigs, through a geometric morphometric analysis of cranial form. Whist the original concept of this study was derived from a grant concerned with the spread of domestic pigs across Europe at the beginning of the Neolithic, this thesis encompasses wider studies. By applying geometric morphometrics to questions of suid evolution and variability and domestication, we can effect a deeper understanding of how pigs colonised Africa, how suid morphology is affected by climate and geography, that wild and domestic pig cranial morphologies are distinct enough to discriminate between. These have implications for evolutionary studies of the suid family, explaining apparent incongruence between morphological studies and genetics. There are significant implications for archaeological studies, especially those concerned with identifying the origins of domestication where inadequacies in the traditional methodology can be overcome through the application of geometric morphometrics. We also test and reject the traditional hypothesis of heterochrony as the causal mechanism for the development of the domestic morphotype.

Methodologies to test this have recently been developed for geometric morphometrics (Mitteroecker et al., 2005), but had not been applied to stock domesticates before. What is seen in suid ontogeny is not explained by the traditional language of heterochrony, nor are domestic pigs paedomorphic wild pigs. This leaves the cause of morphological changes observed during domestication unexplained, which should be a focus of future work.

1.1.1 Structure of the Thesis

This thesis addresses two main themes – biology and domestication – about which GM techniques provide a greater understanding. The thesis comprises an introduction (Chapter 1) discussing the pig-human relationships and the history and current understanding of the key themes, including taxonomy, form and distribution; and the domestication of pigs - what domestication is and how and why pigs were domesticated. Chapter 2 details the GM techniques used to analyse collection of pig cranial material. Chapters 3-6 are the in-depth applications of geometric morphometric analyses to the pig cranial samples, each representing a manuscript for publication. These are each described more fully below.

The first theme focuses on the biology of suids, examined through studies on the evolution of sub-Saharan African pigs (Chapter 3) and biogeography (Chapter 4) of the suid *Sus scrofa*. The second theme focuses on the domestication of pigs: the quantification of cranial morphology, noting differences between wild and domestic pigs (Chapter 5), and the ontogeny of domesticated pigs compared to wild pigs (Chapter 6). The four manuscripts for publication each have research aims and questions discussed in detail:

Chapter 3 – **Resolving phylogenetic and phenotypic relationships within Suidae**

(Manuscript 1)

Phenotypic trees derived from morphology often differ from independently estimated phylogenetic trees, usually as a result of convergent or parallel evolution. Within the family Suidae, there is marked incongruence between the morphologically and genetically derived relationships between the sub-Saharan African genus *Potamochoerus* and the Eurasian *Sus*. Whereas genetic analyses show the monophyly of the sub-Saharan African pigs, morphological analyses suggest that *Potamochoerus* is more closely related to *Sus* than other sub-Saharan pigs. These conflicting interpretations hamper a resolution of the systematics of the suids and confound efforts to understand their colonisation of the African continent. In order to understand the source of the conflicting topologies, we applied geometric morphometrics and multivariate statistics to 38 unilateral homologous landmarks from 471 African and Eurasian suids. We then reconstructed the ancestral node of Suidae and tested the mode of evolution. *Potamochoerus* is phylogenetically more closely related to African genera but like *Sus*, it possesses a generalist morphology and occupies the same ecological niche. This shared generalist behaviour, a direct consequence of the evolutionary history of *Potamochoerus*, is the principal reason for morphology's failure to alone reveal the monophyly of African suids.

Chapter 4 - **Pigs in space: Biogeographic variation in *Sus scrofa*** (Manuscript 2)

Pigs have one of the widest distributions of any large mammal, endemic throughout the Palearctic and Indomalaya. Throughout this range there are recognised morphotypes that have traditionally been described as separate species, mainly on the

basis of size and morphological characteristics. These methods are also the basis of investigations into the species history, including studies of domestication. However most of these studies fail to appreciate all the sources of possible variation present within these measurements beyond sexual dimorphism. It has long been recognised that climate, latitude and longitude are linked to shape and size changes in large mammals. The impact that these variables have on suid morphology have not been systematically quantified in suids across their natural range, recent advances in shape analysis, especially in geometric morphometrics (GMM), make this possible. Here we apply GMM to 429 adult suid crania, including most genera, but concentrating on the most wide spread genus, *Sus scrofa*. Our results demonstrate that environmental and climatic variables are major sources of variation in both cranial shape and size in *Sus scrofa*, with precipitation strongly linked to size change in European pigs. The effect of environmental and geographic variables diminishes as wider geography regions and more species are included, the remaining variance increases, representing factors not tested including genetic variation that could be interpreted as speciation.

Chapter 5 - Quantifying cranial shape differences between wild boar and domestic pigs (*Sus scrofa*) using 3D shape analysis and its application to zooarchaeology (Manuscript 3)

The phenotypic changes caused by domestication are well known. Zooarchaeologists have attempted to study these changes osteologically in their search for the geographic origins and temporal context of the initial animal domestication during the Late Pleistocene and early Holocene. Traditional biometrical approaches have explored changes in body size over time, but give poor resolution and are adversely

affected by factors such as climate, sex, diet and disease. Here we investigate whether geometric morphometric analyses of cranial shape can be used to provide better resolution between wild and domestic pigs (*Sus scrofa*), as we know that shape is less affected by environmental factors than size. Geometric morphometric methods with traditional multivariate statistics were applied to an adult, modern pig cranial sample of 52 domestic and 142 wild pigs. Analyses were also carried out on morphologically discrete portions of the whole skull to simulate the fragmented nature of archaeological mammal remains. Highly significant discrimination was found between wild and domestic pigs from analyses of the whole skull, the parietal, the basicranium, the angle of the nasal and the zygomatic. Our data shows that geometric morphometric techniques could be successfully applied in zooarchaeology to provide a much better, quantifiable resolution between wild and domestic pigs, even on the basis of partial remains.

Chapter 6 - **Domestication and heterochrony in *Sus scrofa*** (Manuscript 4)

Domestication in animals creates a variety of morphologies and behaviours unique to itself. Traditionally these have been explained through the framework of heterochrony: changes in the rate and timing of development. For example the domestic phenotype is often described as paedomorphic, resembling the juvenile ancestral state, caused by the process of Neoteny – reduction in the rate of growth of shape, relative to growth in size. Recent advances in techniques like geometric morphometrics (GM) allow this hypothesis to be tested in a multivariate framework, which have falsified hypotheses of paedomorphism in dogs (Drake, 2011), as well as wider usage to examine cranial heterochrony in hominines and monkeys. Here we examine the theory that heterochrony is responsible for the development of the

domestic phenotype in pigs (*Sus scrofa*). We applied GM methods to three longitudinal ontogenetic series (one wild, two domestic), calculating the angles between ontogenetic trajectories and comparing morphological distances between the series at different ages. We also tested wild and domestic pigs for evidence of paedomorphism, comparing the adult descendent phenotype (six breeds of domestic pigs) to the juvenile and adult ancestral phenotype (wild pigs). We conclude that heterochrony is not sufficient to explain the domestic morphology of pigs, neither is there evidence of paedomorphism in five of the six domestic breeds tested. Thus the traditional explanation of heterochrony as the causal mechanism for the domestic phenotype is wrong, and a new explanation must be sought.

1.1.2 Pig Exploitation

Humans have a long and complex relationship with pigs, ranging from a simple hunter – prey interaction, to the central focus of a community's economy and ritual life (see 1.1.3). The following section of the thesis details some of the reasons why pigs are important to humans, and gives examples of how pigs have been perceived and relate to different societies.

Pigs are today a valuable economic resource, both as a stock domesticate and a game animal (Scandura et al., 2011), and are increasingly being kept as companion animals (McDonald-Brown, 2009). However, pig exploitation dates from before the Palaeolithic and was focused on hunting (Albarella et al., 2007). Although wild pigs are dangerous prey, capable of protecting themselves and their offspring, they represent a high calorific return on the energy expended hunting them (Rowley-Conwy et al., 2002).

As domestic animals, pigs are raised for their meat. They are fast growing, have large litters (Sack, 1982) and, provided the necessary resources – space, shade, food and water – are met, they are a valuable source of protein, particularly good for expanding populations. Unlike other domesticates, pigs have few secondary products such as milk and wool and they cannot be used for traction to pull carts and agricultural equipment.

There is no archaeological evidence of pigs being kept for companionship like cats or dogs, which is primarily a modern innovation. Evidence shows they were kept as a food resource and that their bones were worked as tools and ornaments (see figure 2

below) (Albarella et al., 2007). Modern ethnographic examples of worked pig bone include the items created by the Dani people of Irian Jaya (Hampton, 1999), who make extensive use of this medium. Pig bone knives are made from the tibia, with the cutting edges created using grindstones. These knives are used to cut or divide tubers. Bones knives are used for this task in preference to stone tools, possibly due to the ubiquity of pig bone in the Dani culture or the ease of working it. The Dani also use boar tusks (the male canine) as a scraping tool. This tool is used to smooth spear, axe and adze hafts, as well as digging sticks and arrows. A cutting tool is also made from pig teeth: the inner edges of the tooth are sharpened with chert flakes to create cutting edges, allowing the tool to be used in a to-and-fro action. The ubiquity of the bones and teeth in a pig rich environment, combined with the ease of creating and maintaining the tool makes pig teeth and bone an adaptable resource.

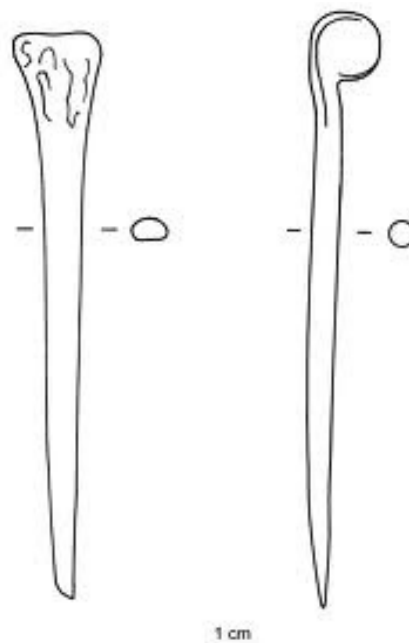


Figure 2: Hair or clothing pins made from pig fibula from medieval Holland (Prummel et al., 2011)

1.1.3 The Extreme Relationships between Pigs and People

Throughout recorded history there have been incidences of extreme human reactions to pigs that are unusual in human-animal relations; these have been termed 'Pig Love' and 'Pig Avoidance' by Marvin Harris (1974). Pig love goes beyond appreciation of the taste and the culinary characteristics of swine flesh: "it is a state of total community between man and pig" (Harris 1974:39). This includes raising pigs as a member of the family, physically and verbally interacting with them, feeding them from the family table and tending to them when sick. This pig love does not preclude ritual slaughter, but raises it to a level of heartfelt sacrifice that separates pig love from the ritual veneration seen in the Hindu relationship with cows. The classic example of pig love is seen in the indigenous peoples of Papua New Guinea, such as the Maring, who operate on a cyclical system of internecine clan warfare. This relationship centres on a ritual known as *kaiko*, which consists of small scale pig offerings preceding a larger ritual sacrifice. In the build up to the *kaiko*, the clans go to war, which is characterised by pig sacrifice to implore the ancestors to intercede in a particular scheme or battle. The result is the almost total eradication of the adult porcine population, which signals the cessation of hostilities and the rebuilding of the pig population until the next *kaiko*. Almost all aspects of the Maring culture is based around pig rearing, providing for them and protecting them, so that the clan is able to start their next *kaiko* richer in pigs than their rivals and thus able to sustain hostilities longer than their opponents (Harris, 1974). This example of pig love is unusual, but indicative of the sometimes high esteem in which pigs can be held.

The opposite case to pig love, pig avoidance, is perhaps better known, in particular the taboo on the consumption of swine flesh upheld by the Jewish and Islamic

religions. This taboo is a total ban not just on eating pork or using pork products, but also on interacting with pigs in any way. Should a member of these religions come into contact with a pig then, according to some doctrines, a complex series of ritual cleansings needs to be followed. In Judaism permissible foods are called Kosher; meat must be from a ruminant which has split hooves. The Torah gives two passages relating to pigs:

And the swine, though he divide the hoof, and be clovenfooted, yet he cheweth not the cud; he is unclean to you. Of their flesh shall ye not eat, and their carcase shall ye not touch; they are unclean to you (Leviticus 11:7-8)

And the swine, because it divideth the hoof, yet cheweth not the cud, it is unclean unto you: ye shall not eat of their flesh, nor touch their dead carcase (Deuteronomy 14:8)

For followers of Islam, the Quran prohibits the consumption of pork:

He has made unlawful for you only (carcass) that which dies of itself and blood and the flesh of swine and that on which the name of any other than Allah has been invoked. But he who is driven by necessity, being neither disobedient nor exceeding the limit, then surely, Allah is Most Forgiving, Merciful (16:116).

The reasoning for such religious taboos is not clear. That pigs are non-ruminants without cloven hooves is descriptive, not explanatory; neither religious text states why these animals should be avoided. It is possible that cleanliness is a causal factor: pigs roll around in mud or urine to cool down as they have fewer sweat glands than other large mammals (Hafez, 1968, Sack, 1982). Pigs are also omnivorous and will eat refuse; however, so will chickens, which are not banned, but also do not have pigs' reputation for being dirty animals. Harris (1974) suggests that ecological or

economic reasons explain the pig taboo. Pigs are not well adapted for the Middle East, where the cores of these religions are located. Pigs require a constant water source and shade from direct sun light (Hafez, 1968), occupying woodland in which to forage and root. These needs place them in direct competition with humans for scarce water and land resources. Urban pigs kept by individual families in towns and cities could partially remove the families from the market based taxation system as the pigs could enable them to produce their own meat. It is possible that these factors resulted in a prohibition against pig keeping with the pretence of hygiene as the reason.

1.1.4 Pigs and Social Status

Pigs have often been associated with social status; specifically they are seen as a marker of wealth. The lack of secondary products and the intensive food and land requirements needed to raise them meant that in societies where adequate land for foraging was not available pigs became a status symbol. This situation is evident in the British Iron Age where some areas of Britain were unsuitable for pig rearing, making the presence of pig rearing indicative of conspicuous consumption. In the Scottish Western Islands pigs comprise of between 6-16% of mammal faunal assemblages in wheelhouses and 18-40% in the higher status brochs (Parker-Pearson, 1999), demonstrating that pigs were reared as status symbols, items of power.

1.2 The Biology of Pigs

Pigs are ungulates; they walk on the tips of their hoofed digits, of which they have four: two principal ones (III and IV) and two accessory ones (II and V) (Sack, 1982). As such they are members of the artiodactyls like cows, sheep and goats, although pigs are not ruminants. Their closest relatives are the Tayassuidae (Peccaries) which fill a similar niche to pigs on the American continent. The next closest relative is the Hippopotamidae of Africa (Oliver, 1993).

1.2.1 Current Taxonomy

The family Suidae consists of four sub-families: the Babirusa (*Babyrousa*), the Phacocherinae (*Phacochoerus*), the Suinae and the Porcula (Groves, 2007).

Babyrousa contains three recognised species: *B. celebensis*, *B. togeanensis* and *B. babyrussa* (Meijaard and Groves, 2002b). *Phacochoerus* contains two species (Grubb, 1993b), the common warthog (*Ph. africanus*) and the Cape and Somali warthogs (*Ph. aethiopicus*; now extinct around the Cape). Porcula contains a single genus, *P. Salvania*, the Nepalese pygmy hog that was established as a monotypic genus by (Funk et al., 2007).

The Suinae contains three genera: *Hylochoerus meinertzhageni* (the giant forest hog) which includes three subspecies, *H.m. meinertzhageni*, *H.m. rimator* and *H.m. ivoriensis* (Grubb, 1993b); *Potamochoerus* which contains two recognised species, the African bush pig (*P. larvatus*) and the red river hog (*P. porcus*) (Grubb, 1993b); and *Sus*.

Sus contains seven main species. The most wide spread of these is *Sus scrofa* which is endemic to the majority of Eurasia (Groves, 2007). The remaining species, along with *S. scrofa*, are all found in Island South East Asia (ISEA) and comprise *S. philippensis*, *S. celebensis*, *S. verrucosus*, *S. barbatus*, *S. ahoenobarbus* and *S. cebifrons*. These are split into two main groups: the warty pigs (*S. philippensis*, *S. celebensis* and *S. cebifrons*) and the bearded pigs (*S. verrucosus*, *S. barbatus* and *S. ahoenobarbus*) (Cucchi et al., 2009, Groves, 1981, Groves, 1997). There are two additional minor species that are critically endangered: *S. bucculentus*, the Vietnamese warty pig (Groves and Schaller, 2000); and *S. oiveri* of Mindoro in the Philippines (Groves, 1997).

Sus scrofa consists of 16 subspecies (Groves, 2007) that can be split between Europe and the Near East on the one hand and South East Asia on the other on the basis of genetics (Hongo et al., 2002, Kim et al., 2002, Larson et al., 2005). Morphologically *Sus scrofa* is split into four main groupings (Groves, 1981), although the boundaries between them are not clearly delineated: the ‘Western’ group of Europe and Near Eurasia (including *S.s. scrofa*, *S.s. attila*, *S.s. nigripes* and *S.s. meridionalis*) and North Africa and the Middle East (*S.s. algeria* and *S.s. lybicus*); the ‘Indian’ group from Iran to Thailand (*S.s. cristatus*, *S.s. davidi* and *S.s. affinis* whose taxonomic status is debated); the ‘Eastern’ group of Mongolia and Russia to China and Vietnam (*S.s. sibiricus*, *S.s. ussuricus*, *S.s. moupinensis*, *S.s. leucomystax*, *S.s. riukiuanu* and *S.s. taevanus*); and the ‘Indonesian’ group from the Malay peninsula through the Indonesian islands (*S.s. vittatus*) (Groves, 2007, Groves, 1981). This thesis goes on to show the phylogeny and morphology of *Sus* are complementary; the different phylogenetic groups, identified in Larson et al (Larson et al., 2005) map onto the

morphological designations: the differences between Eastern and Western type pigs being far greater than the differences within the Eastern type clades (the Indian, Eastern and Indonesian groupings).

In this thesis only the following genera were studied: *Ph. aethiopicus*, *P. porcus*, *P. larvatus*, *B. celebensis*, *S. scrofa*, *S. celebensis*, *S. cebifrons*, *S. philippensis*, *S. barbatus* and *S. ahoenobarbus*. This was due to availability of material.

1.2.2 Geography, Ecology and Habitat of the Suids Studied

Of the African pigs, *Ph. aethiopicus* is found in south-eastern Ethiopia, western Somalia, and in central and eastern Kenya where it inhabits open, arid regions from bush and open woodland to sub-desert steppe (d'Hart et al., 2008). Along with its sister species *Ph. africanus* (found throughout the sub-Saharan African savannah) it is adapted to savannah habitat and grazing behaviour. They are omnivores like all suids; eating bark, fungi, berries and carrion but specialising on perennial grasses, bulbs and roots (Estes, 1991). *P. porcus* is widely dispersed through the west and central African rainforest, in habitats ranging from mature and gallery rainforest to dry savannah woodland and cultivated areas (Querouil and Leus, 2008). *P. larvatus* inhabits the southern Sudan, Ethiopia and Eritrea and southwards throughout east Africa, mostly to be found in areas of dense vegetation (Seydack, 2008). Both *Potamochoerus* species are typical suid omnivores, their diet focusing on grasses, water plants, roots, bulbs, fruit, carrion and small animals (Vercammen et al., 1993).

All *Babyrrousa* species inhabit the tropical rainforest of Sulawesi, in areas with good access to water and are now confined to more remote inland areas (Groves, 2001,

Meijaard and Groves, 2002a). *B. celebensis* is found on mainland Sulawesi, while *B. togeanensis* and *B. babyrussa* are found on the Togian archipelago and the Sula Islands respectively. Babirusa are all omnivorous, although the absence of the rostral bone suggests that they do not root like other suids (Macdonald, 2010a). They consume a wide variety of fruit, root and animal matter (Macdonald, 2010b, 2010c) though their diet includes a higher proportion of fruit than other pigs.

S. scrofa is the most widely distributed of the wild suids, its natural range extending from Western Europe to Japan, and from Siberia to the Southern Indonesian Islands (Polly and Eronen, 2011) although its range has suffered significant fragmentation. It is found in a wide variety of habitats, from semi-desert to tropical rainforest to the temperate woodland of Eurasia, its adaptability and widely omnivorous diet (ranging from roots to molluscs to small vertebrates) having allowed it to become the most populous of the family Suidae (Oliver and Leus, 2008).

Sus species other than *S. scrofa* are restricted to the islands of South East Asia. *S. celebensis* is found on Sulawesi (Burton and Macdonald, 2010) and *S. cebifrons* (Oliver, 2010b) and *S. philippensis* in the Philippines (Oliver and Heaney, 2010). *S. celebensis* and *S. philippensis* inhabit forests at almost any altitude, whilst *S. cebifrons* prefers forest at lower altitudes. The main bulk of their diets are roots, fallen fruit, leaves and shoots; carrion, vertebrates and invertebrates are consumed as well (Burton and Macdonald, 2010). *Sus barbatus* and its sub species are found mainly on the Malay peninsula (*S.b.oi*), Sumatra and Borneo (*S.b.barbatus*) (Kawanishi et al., 2010, Lucchini et al., 2005) whilst *S. ahoenobarbus* is found on Palawan (Oliver, 2010a). Both types favour tropical forest but *S. barbatus*

demonstrates the capacity of suids to inhabit a wide variety of habitat types, being found from beaches to upper montane cloud forest (Caldecott et al., 1993). They both consume roots, fungi, turtle eggs and a wide variety of plant material, the most important of which is fruit (Caldecott et al., 1993, Kawanishi et al., 2010).

1.2.3 Evolutionary History of Suids

Pigs have a deep evolutionary history. The superfamily Suoidea (which includes extinct suids and *Sus*) is thought to originate from South-East Asia during the Eocene (Orliac et al., 2010). The ISEA region that today has the highest suid diversity, possibly as a result of sea level fluctuations isolating communities on the islands in the early Pliocene (Lucchini et al., 2005). The ancestors of the Babyrousinae and Suinae lineages diverged from their common ancestor in South East Asia. The Suinae then radiated across Asia, with further divergence occurring as the ancestral suid of *Hylochoerus*, *Potamochoerus* and *Phacochoerus* colonised Africa (Gongora et al., 2011), with the ancestral suid of *Sus scrofa* radiating through Eurasia.

The first evidence of *Sus* reaching Europe dates to 1-1.5 million years ago, in the form of fossils from Italy (Rook and Martinez-Navarro, 2010). Divergence between European and Asian wild boar haplotypes occurring sometime around 900,000 years BP (Kijas and Anderson, 2001, Fang and Andersson, 2006). Suids retreated from much of mainland Europe during the last glacial maximum, surviving in refugia in the Iberian Peninsula, Italy and southwest Europe (Sommer and Nadachowski, 2006), although the extent of their range during this period is not fully established. Re-colonisation of mainland Europe occurred soon after the retreat of the glaciers, leaving biogeographic divisions in the animal's mitochondrial DNA (Fang and

Andersson, 2006, Scandura et al., 2008). Since industrialisation, suids have suffered from overhunting and fragmentation of their habitat, leading to localised extirpation and subsequent reintroduction of neighbouring populations (e.g. Britain) that has led to a recent (post World War II) increase in population. Despite the intensification of farming hybridization between wild and domestic stocks appears to be rare. Certainly the presence of domestic genetic markers is low in modern wild stock (Oliver and Leus, 2008, Scandura et al., 2011), thus any genetic biogeographic signals in wild stocks should still be present, as appears to be the case in the study by (Larson et al., 2005).

1.2.4 Known Biogeographic Variation within *Sus scrofa*

The most widely studied causes of variation in suid morphology and size have been taxonomy (Groves, 1981, Genov, 1999) and domestication (Albarella, 2002, Payne and Bull, 1988, Zeder, 2006a). Variation in form has also been mapped through the Holocene, to reconstruct the history of *Sus* (e.g. retreat into peninsula refugia) and the effect of changing climate on body size through this period (Albarella et al., 2009),

As described above in the suid taxonomy section (1.2.1), morphologically *Sus scrofa* is split into four main groups: the Western group, the Indian, the Eastern and the Indonesian (Groves 2007, Grubb 1993a). These groups fit tolerably well with the known mitochondrial phylogeny of *Sus* (e.g. Larson et al 2005) which shows separate maternal lineages in the geographic regions proposed by studies on morphology (see figure 3 below).

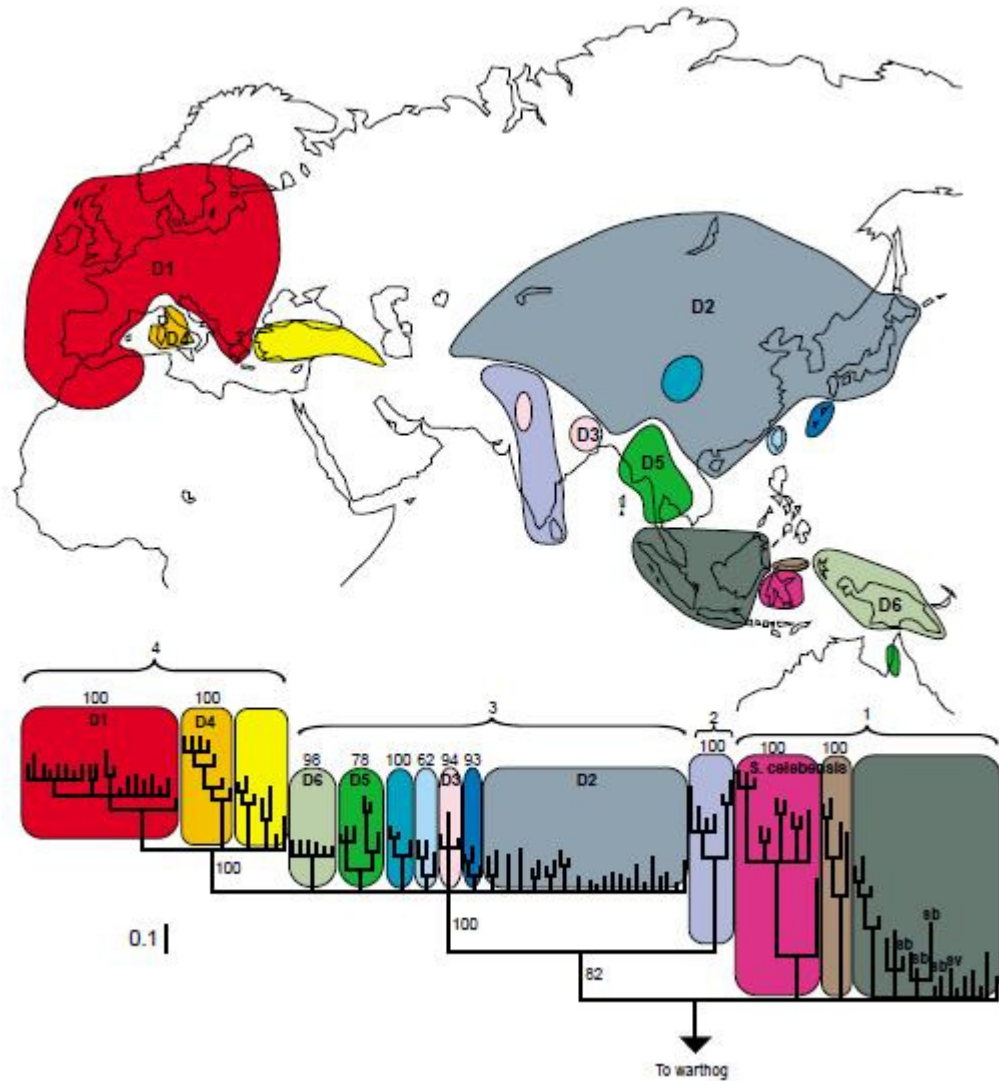


Figure 3: Distribution of *Sus* haplotypes (Larson et al., 2005)

Most known biogeographic variation in pigs is based on differences in size. In Europe, size increases from west to east and south to north (Albarella et al., 2009). Size increases in eastern Europe have been attributed to ‘continentality’ – harsher winters in the east having an increased bottlenecking effect, reducing intra-specific competition (Weinstock, 2000). The south-north size increase is driven, and explained by, the presence of larger pigs in the Near East, although why pigs should be larger in the Near East is currently unexplained (Albarella et al., 2009).

(Davis, 1981) surveyed extant and past pig populations (amongst other animals such as Aurochs, dogs, foxes, gazelles and goats) in the Levant, noting a negative temperature-size relationship in modern populations, coupled with size decreases in pigs at the end of Pleistocene, and another size decrease associated with domestication. Davis attributes size decreases to Bergman's rule in wild pigs, foxes and dogs, noting that the regression lines of log dental size on temperature are similar in these species. The Pleistocene size reduction (present in all the animals Davis examines) is explained by the changing climate (e.g. lower temperatures) at the end of the late glacial maximum, which occurs at the Pleistocene/Holocene transition.

(Endo et al., 2002) examined wild pig mandibles (*Sus scrofa*) from Japan, Taiwan and Iriomote Island, noting similarities in size between Taiwanese and Japanese pigs from Honshu and the environmental effects of latitude and elevation on shape. Little further work has been conducted on other potential influences on morphological variation in pigs, especially the effects of climatic or geographic variables such as moisture and temperature or latitude and longitude on suid shape and size across the wider extents of the *Sus scrofa* range. In manuscript 2 I attempt to address this gap, analysing pigs from across Eurasia and analysing how cranial variation is affected by climate and geographic variables, and what proportion of variation they explain.

1.2.5 Known Constraints of *Sus scrofa* range

Although *Sus scrofa* is found in a wide variety of habitats it cannot tolerate temperatures above 35°C (95°F) with humidity above 65% without shade and water. This intolerance is known mainly through experiences of the transportation of domestic livestock and is due to a lack of sweat glands and thick layers of

subcutaneous fat (Hafez, 1968). Alleviation of high temperatures in the wild are sought through seeking shade and wallowing in mud or water, thus wild pigs are rarely found far from water and shade (Oliver, 1993) even in semi-arid environments. Frozen ground and deep snow also limit the range of *Sus*, limiting mobility and the ability to acquire food through rooting. Pigs never crossed the ‘Bering filter’ to reach North America and are only found in Eurasia, Oceania and Africa (Finlayson, 2004).

The main mechanism of population regulation is intra-specific competition for food or space governed by stochastic environmental factors (Uzal and Nores, 2004). This is reflected in the preference of *S. scrofa* to inhabit areas of energy rich foods (Massei and Genov, 2004).

1.2.6 Suids and Insularity

Pigs exhibit the classic response of large mammals to insularity and the ‘island rule’—dwarfism (Millien et al., 2006, Meiri et al., 2011). Recent studies of body size extremes have shown that while examples of insularity are not as numerous as once thought, large animals are one group for which the island rule holds true (Meiri et al., 2011). In pigs the effects of the island rule are seen on many of the islands where pigs are found, including Corsica and Sardinia (Albarella et al., 2009), ISEA (e.g. *Sus ahoenobarbus* (Oliver, 2010a) and the islands off-shore from Japan and Taiwan (Endo et al., 2002).

The (Endo et al., 2002) study on pigs from Taiwan, Honshu (Japan) and Okinawa found that the size of the pig was linked to the size of the island. The smallest pigs

were found on Iriomote Island (part of the Okinawa Islands) which is 289 km², while pigs were larger on the Islands of Honshu (227,963 km²) and Taiwan (36,193 km²). The relationship between island size and pig size is not absolute, as the second smallest pigs are found on Corsica and Sardinia, which are larger than the Japanese islands, and on some larger islands (e.g. Ireland) there is no dwarfing at all (Albarella et al., 2009).

Reasons for dwarfism on some islands and not others may depend on the island itself, especially its area and isolation, the climate, geology (e.g. whether they are part of the continental shelf, part of a tectonic plate or volcanic) and the biogeographic settings (e.g. realm, ocean) (Meiri et al., 2011). Crockford (2002, 2006) attributes the expression of dwarfism and gigantism to thyroid hormone rhythm in conjunction with stresses unique to islands (e.g. habitat, founder effect and diet). She contends that having stress-tolerant individuals as a large part of the founder population explains the variability of expression of the 'island syndrome' as stress-tolerant phenotypes, with thyroid hormone rhythms and associated growth patterns typically generate early maturation at smaller sizes (Crockford, 2006). Yet the role of thyroid hormone is hard to pinpoint in specific changes, partially because of its complexity, and partially because it is so pervasive in all aspects of development (Dobney and Larson, 2006). As Crockford suggests, further research is needed to establish its role.

Pigs have been introduced to many islands outside of their natural range by humans, including the introduction of pigs to Cyprus in the Epipaleolithic (Vigne et al., 2009), Ireland during the Mesolithic (McCormick and Murray, 2007) and Corsica and Sardinia in the Neolithic (Albarella et al., 2006b). During these introductions pigs

must have been under human supervision during transportation before release as hunting stock, but would still be wild animals. However, in some cases it may be that domesticated animals were transported and released as feral animals, providing an explanation for the situation on Corsica and Sardinia where wild, feral and domestic animals are found as a result of a domestic introduction (Rowley-Conwy, 2011).

These early island introductions also violate the assumption that animals found outside of their natural range must be domestic – the Cypriot and Ireland introductions occur long before the innovations of agriculture or domestication had reached these areas. Thus the establishment of the status (wild or domestic) of original founder populations could be significant to studies of the origins and spread of domestication.

1.3 Domestication

Domestication is a process that facilitated the transition from hunter-gathering to sedentary farming. As such it is one of the crucial developments in the creation of modern society. Domestic plants and animals first appeared in South-West Asia around 12,000 years ago at the start of the Neolithic Revolution, a suite of widely encompassing changes experienced by humans at the end of the last ice age. The Neolithic Revolution describes the change from a hunter-gatherer lifestyle to that of agro-pastoralists, which includes the development of sedentary societies with associated technology such as pottery, specialised food production techniques like irrigation and transhumance, art, architecture and trade (Bellwood, 2005).

The change from hunter-gatherer to agriculturalist is one of the seminal moments of human history. Vigne described neolithisation as follows:

Characterized by the start of an unprecedented increase in human activity and its subsequent impact on the environment. It is marked by the birth of new types of ecosystems including those strongly impacted by humans (man-modified ecosystems, e.g. exploited forests) and those distinctly artificial (manmade ecosystems, e.g. agrosystem, village, city). (Vigne 2011a:177)

The Neolithic Revolution was first described by Vere Gordon Childe (1925, 1936) who postulated that climate change at the end of the Late Glacial Maximum forced humans and animals together into ‘Oasis’ of more stable resources. This theory has been superseded. The most common modern hypothesis focuses on climatic amelioration producing warmer, wetter, more favourable climatic conditions that caused hunter-gatherer populations to expand, forcing them to propagate wild plants, which became the ancestors of domesticated plants (e.g. rye, wild lentils). The

subsequent onset of the Younger Dryas and the loss of favourable climatic conditions may have reinforced the reliance on cultivated plants to offset fluctuations in the availability of wild resources (Bellwood, 2005).

One of the hypotheses directly relevant to animal domestication is that of human niche construction (Vigne, 2011a, Rowley-Conwy and Layton, 2011). Human niche construction caused changes in the local environment to enable increased reproduction in wild animals making them a more reliable food source. In a 'disturbed' climate, such as that of the Younger Dryas, niche construction would be an attractive subsistence strategy. The closer relationship between humans and animals started the process of domestication, leading some authors to describe situations either where wild animals and plants adapt to humans in a symbiotic relationship (Rindos, 1980), or where humans begin to manage plants and animals as 'proto-domesticates'. In turn, humans would have been selected (via cultural evolution) or motivated (via rational choice) to modify their behaviour so as to favour the propagation and growth-multiplication of these proto-domesticates (Vigne, 2011a).

There would not have been a straight forward shift from hunting and gathering to food production. (Reading, 2005) explains that the normative paradigm – one of progression, fast or slow and possibly including intermediate steps of cultural control or proto-domestication – does not account for failure or different tactics during the process of neolithisation. He proposes an alternative paradigm whereby there were dead ends and failed experiments and that it may be possible to see these in the archaeological record. Thus the process of neolithisation and/or domestication is one

of faltering steps, often retracing itself or starting again. As such, it is not a simple additional episode in biological evolution but a discontinuity in the evolution of the biosphere (Vigne, 2011a). That is, humans, as a species, became able to modify their surrounding environment using socialized (i.e. flexible) techniques. The main difference between human niche construction and classic biological processes is the element of human intent (Zeder, 2009).

The question of intent, of how much humans deliberately intervened in the lives of animals, has been a central point in the discussion of domestication (Zeder, 2006c, Jarman, 1976a). The ‘balance of power’ in the domesticate-human relationship is contentious. Some have argued that the emphasis should be placed on the human role as masters of animals, exercising a form of cultural dominance, implying that these creatures are forced to live and multiply in captivity; the animals acquire domestic traits as a result (Gautier, 1990). Others theories have postulated that animals ‘chose’ domestication or were willing participants in the process, gaining equally from the arrangement. The theories are focused on the mutualistic aspects of domestication; (Rindos, 1980) notably postulated this latter for plants and it has also been suggested for animals (Higgs and Jarman, 1972). Other mechanisms, such as social parasitism (where one community exploits another), have been proposed for relationships with particular animals e.g. the domestication of reindeer (*Rangifer tarandus*) (Zeuner, 1963), but are limited to specific cases. The overarching point is best summed up by (Meadow, 1989) who characterized domestication as a change of focus on the part of humans from the dead to the living animal and, more particularly, from the dead animal to the principal product of the living animal – its progeny.

1.3.1 Defining the Process of Domestication

Domestication has been defined many times, each emphasizing a different component of the human-animal relationship (Arbuckle, 2005). The problem with each definition is the inherent difficulty in assigning static terms to a process involving long-term and continuous changes (Dobney and Larson, 2006). It is difficult to formulate a definition of domestication that is general enough to account for the wide variation observed in different species, in different captive environments, yet specific enough to be meaningful in terms of the biological processes involved (Price, 1984). Thus no single definition of domestication has been adopted by the scientific community studying it, with many papers having to dedicate a section to explain how the authors are approaching the definition of domestication in each case.

Definitions of domestication have fallen into two main categories as defined by the field of lexical semantics (Dobney and Larson, 2006); complementaries and antonyms. Complementaries are mutually exclusive e.g. open/closed. Antonyms are pairs of opposites that are gradable e.g. fast/slow. Both approaches have been used to define wild/domestic, but the antonym approach, that of a scale between wild and domestic has been favoured.

The change in language describing domestication has followed a greater awareness that the process of domestication is generally slow and not fast (Ervynck et al., 2001): that there is no sudden switch from wild to domestic and that it may be graded. (Zeuner, 1963) identifies 5 stages of domestication:

1. Loose contacts, with free breeding;

2. Confinement to human environment, with breeding in captivity;
3. Selective breeding organized by humans, to obtain certain characteristics, and occasional crossing with wild forms;
4. Economic considerations of humans leading to the planned ‘development’ of breeds with certain desirable properties;
5. Wild ancestors persecuted or exterminated.

These stages emphasise the increasing intensity of domestication through which a species would pass through time.

Although creating another standard accomplishes little more than creating a proliferation of standards¹ it is important to clearly set out domestication is defined for the purposes of this thesis:

Domestication is an *anthropogenic* process whereby humans and animals enter a symbiotic relationship of mutual exploitation and benefit.

The key term here is *anthropogenic*; this is a human orientated and initiated process but is one that has huge benefits for the animals involved. Humans gain a regular and reliable source of food and ‘secondary’ products such as milk and other dairy products, skins (e.g. leather) and other raw materials such as bone (for tools or glue). Animals gain protection from predators and the environment and a regular and reliable source of food. Although it may seem odd for animals to ‘benefit’ given many of them end up slaughtered, many individual animals end up living far longer than they would in the wild where illness or old age would leave them vulnerable to predation. As a species, the domesticates range far beyond their natural range (Rowley-Conwy et al., 2012), moving into to new habitats behind natural barriers

¹ <http://xkcd.com/927/>

beyond their ability to negotiate². While this may be of little solace to slaughtered individuals, it has resulted in species that have become far more successful³ with human intervention than they would ever have been without.

An advantage of this definition of domestication is that it captures the entire range of domestication, from the first stages of domestication moving beyond the hunter-prey relationship to the ‘fully’ domesticated, genetically modified modern breeds. The hunter-hunted scenario is not included as part of the domestication process as there is no ‘benefit’ to the hunted population barring possibly reducing intra-specific competition. One major issue unresolved is where along this continuum animals become ‘domestic’, the crux of the matter being how to define ‘domestic’.

1.3.2 Defining a ‘Domestic’ Animal

What constitutes a domesticated animal? (Clutton-Brock, 1988:32) defines it as “one that has been bred in captivity for the purposes of economic benefit to a human community that maintains total control over its breeding, organization of territory, and food supply.” (Gentry et al., 2004) expands this definition and describes four characteristics of ‘developed’ (i.e. modern) domestic animals: (1) its breeding is under human control; (2) it provides a product or service useful to humans; (3) it is tame; (4) it has been selected away from the wild type. Yet there is clearly a range of ‘domesticated’ animals that do not come into this envelope, including tame animals (as individuals or as groups) not providing product or service’ feral or semi-feral animals; or a variety of degrees of domestic animals where humans do not have ‘total’ control of breeding, territory or food supply, but exert enough control to

² E.g. the introduction of sheep (*Ovis aries*) and goats (*Capra hircus*) into Europe.

³ Success is measured here by increase in range, increase of population and the continuation of inherited genetic lineages that may or may not be the purpose of existence.

organise groups of animals. An example of this last is given by (Albarella et al., 2006a) of early 20th century urban pigs in Britain. Allowed to wander freely through townships and forage (and presumably mate) for themselves, they do not fulfil Clutton-Brock's criteria for domestic animals, yet their owners would recognise them as 'domestic' animals. Clearly, defining a domestic animal is problematic.

This is particularly a problem in studies of the earliest domestic animals. There is inevitably a stage where animals are primed for domestication due to their proximity to human settlements, or the early stages of management of localised wild populations in the early stages of human niche construction (Vigne, 2011b) yet where is the threshold where an animal is no longer wild and has become domestic? Labels to describe half-way houses have been created' including 'proto-domestic'; yet to an extent these duck the issue (Zeder, 2006c), and perhaps it is better to appreciate that the animal and society is on the way to domesticating animals, rather than to worry about how far along the path they have come.

As such, whatever label is applied, ultimately we are best served by thinking of domestication as a scale, with 'wild' animals that have never seen or come into contact with a human at one end, and 'fully domesticated' animals that are a result of intensive breeding programs and spend their entire lives in captivity at the other (fulfilling (Gentry et al's., 2004) four characteristics defining developed, modern domestics). Feral animals, that is domesticated animals that have escaped or been released, reach beyond the domestic side of the scale, even if they subsequently revert to 'wild' status. An example of this scale is graphically produced below (Figure 4: reproduced from (Vigne, 2011a)). Although the issue of where along the

continuum an animal becomes ‘domestic’ is not resolved, it may be that it is too ‘local’ an issue to apply a global rule, and as such a ‘domestic’ label is applied on a case by case basis.

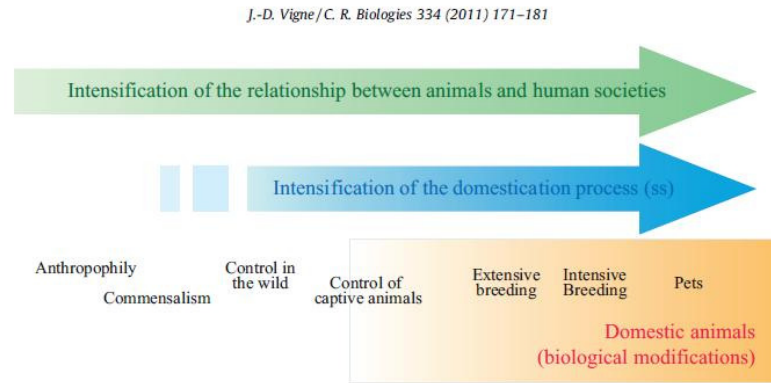


Fig. 1. Domestication can be considered as an ultimate phase of intensification in the relationship between animal or plant sub-populations and human societies. It is comprised of several grades of intensification that, by various means and over varying periods, may end with the emergence of domestic animal as well as plant and microorganism lineages shaped by humans. The control of wild animals is a form of domestication that does not entail any visible morphological modifications, at least from an archaeology point of view.

Figure 4: Representation of the scale of interaction between animals and humans, from (Vigne, 2011a)

The role of tameness is been an important consideration in the process of domestication. Tameness can be achieved by habituation, positive associative conditioning, and it may be attained without any deliberate human effort. In habituation the animal's fear of humans is gradually reduced by repeated exposures in a neutral context; that is human presence has neither positive nor negative reinforcing properties. Positive associative conditioning occurs when the animal's fear of humans is reduced by humans acting as providers of food, water, shelter, and grooming. Humans become secondarily associated with positive stimuli and the threshold for avoiding people is raised (Price, 1984). Thus the initial role of taming could be an important step on the ‘path’ to domestication.

However, Melinda Zeder points out, it is important not to get too focused on the exact demarcation between wild and domestic in any given context:

To some extent, it remains a matter of personal preference to decide just when a domestic subsection of a plant or animal species has been created. Threshold criteria that require total genetic isolation and emergent speciation or complete dependence on humans for survival set a very high bar that many, if not most, widely accepted domesticates would fail to clear. Even somewhat looser standards that involve a lesser degree of genetic modification in the target plant or animal population, or a certain level of human investment in propagating, nurturing, or owning the resource, run the risk of constructing artificial boundaries along what was really a more seamless incremental process. (Zeder, 2006b:107)

Thus the argument as to at what precise point in time we have actual ‘domestic’ animals (whatever they are) is distracting from the real focus of study – the process of domestication itself. What sort of evolutionary process is it? And what are the effects? And how and why does it occur?

1.3.3 How do Animals Become Domesticated?

It is quite possible for individual members of a species to become tamed or accustomed to human presence, but for domestication to occur these individuals must breed and their offspring and successive generations become viable breeding animals as well (Price, 1984, 1999).

Six physiological and behavioural conditions have been proposed by (Clutton-Brock, 1999), expanding on work by (Galton, 1865) and (Guppy, 1961), for animals to fulfil if they are to become domesticated. These are:-

1. Hardy; the animals have to adapt to new environments, diets and often conditions which are more conducive to infection than their natural state.
2. Social; in most cases (cats being the most obvious exception) humans become the dominant member of the group, thus creatures that are social by nature are far easier to domesticate.
3. Reduced flight response; or it must be easily suppressible, as animals with a strong flight response (antelope, gazelles and deer) do not eat or breed well if constrained.
4. Useful; the animal must have an obvious primary purpose, be it as food (pigs, sheep, goats and cattle), a hunting aid (dogs), pest control (cats, ferrets) or locomotion (horse).
5. Breed freely; the most important factor for domestication. Captive breeding is tricky even under favourable conditions such as modern zoos, thus if a species does not freely breed the chances of successful domestication is low.
6. Easy to tend, gregarious and placid animals with a varied diet are easier to maintain and herd (and thus protect), thus minimising input.

Given the stringency of these conditions it is not surprising that only a few species have been domesticated. It is known that the ancient Egyptians attempted and failed to domesticate some species like gazelles and hyenas (Zeuner, 1963), and it is probable that similar failed experiments were conducted at many points in human history. But pigs curious, intelligent and gregarious nature; resistance to disease and

general hardiness; quick breeding and high return of meat vs. resource input makes it not surprising that they were one of the first animals domesticated.

1.3.4 Domestication Pathways

It is likely that pigs followed a domestication trajectory closer to that of dogs rather than those of sheep, cattle or goats (Clutton-Brock, 1988, 1999). In the initial relationship each population adjusted to the presence of the other, in the case of pigs they became used to the permanent human camps while humans became used to the local populations of wild boar (Albarella et al., 2006a). Tamer or braver individual pigs would approach the human settlements, perhaps attracted by scavenging opportunities. These may have been hunted or welcomed, treated as pets or accepted into family groups as in the pig loving cultures of Papua New Guinea (Dwyer, 1996). Regardless of the response, physiological and phenotypic changes would already have begun to reshape the local wild population, but it was not until humans began to purposefully capture and breed animals, and thus enhance selective pressures on that domestic population, that true domestic pigs were created.

This type of pathway has been labelled a commensal pathway, animals that came into contact with humans to scavenge or to prey on the scavengers (Zeder, 2012) and include dogs, cats, mice and chickens as well as pigs. Those animals that proved useful were accepted and encouraged, with people gradually taking a more active role in their breeding habits, seeking to encourage desired traits. Not all commensal animals became domesticated, remaining pests (e.g. mice). The main alternative pathways are directed, or prey, as summarised in figure 5 below.

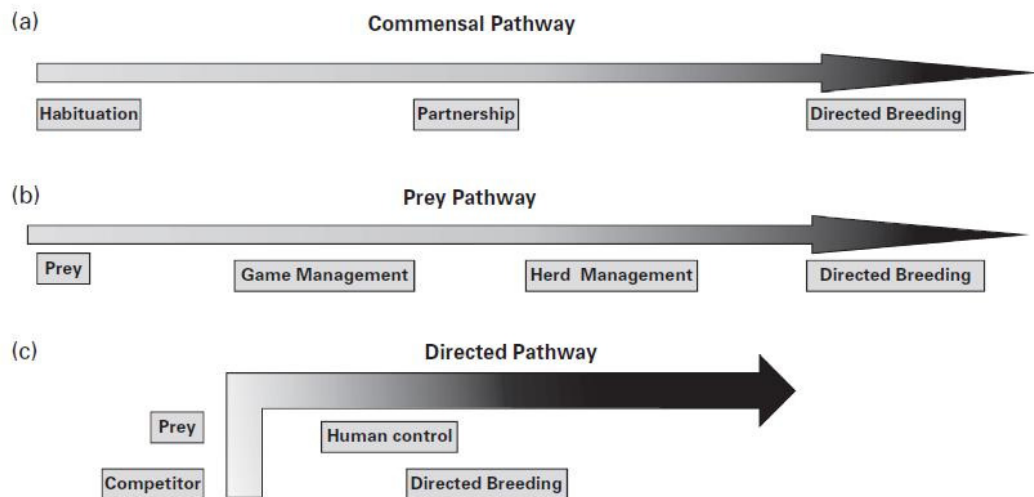


Figure 9.7. Pathways to domestication. (a) Commensal pathway, (b) prey pathway, (c) directed pathway.

Figure 5: Summary of the main types of domestication, from (Zeder, 2012)

Domesticates originally targeted as prey may have become domesticated in response to overhunting, with humans propagating food resources and providing shelter from predators or competitive hunting groups to maintain a stock of food to fall back upon in hard times. Evidence of management of domesticates is seen in the demographic profiles of early Neolithic goat herds of the Zagros (Zeder, 2005, 2006a), with a predominance of young males and mature females suggesting a focus on herd growth, keeping only a few healthy males and focusing on breeding females. Most of the major domesticates would have followed the prey route like cows, sheep, goats, water buffalo, yak, llama and perhaps reindeer.

Animals on the directed pathway may have begun their route to domestication as prey species, but became utilised for other purposes. For example sheep also produce wool and milk, and evidence for exploitation for milk goes deep into the Neolithic (Evershed et al., 2008) suggesting that soon after domestication the potential for

secondary products was quickly realised. Other reasons for directing animals to become domesticates include transportation (e.g. the horse), traction (donkeys/camels) and pelts (e.g. mink). There are potential niche routes, or individual cases that do not fall into individual or multiples of these routes, like elephants which are more like tamed captives (Zeder, 2012), and already mentioned failed experiments in domestication like cheetah, or gazelles and deer, animals in which the flight response is too great to successfully breed out.

1.3.5 Cultural and Biological Processes of Domestication

1.3.5.1 Cultural

The cultural aspects of domestication deal with how human society changed to accommodate domestic animals. In order to be domesticated, animals have to be incorporated into the social structure of a human community and become objects of ownership, inheritance, purchase and exchange (Clutton-Brock, 1999). The relationship is changed from mutualism, where the environment and its resources are shared to one of domination, whereby humans control resources and access to them. It is for this reason that societies where animals are treated as equals and revered (e.g. totemic societies like the North-West American Coast Indians) never developed domestication (Vigne, 2011b, Ingold, 1994).

1.3.5.2 Biological

The biological changes that occur in domestic animals begin when a small number of individuals are separated off from the wild species. If they successfully breed and become used to human company they will form a founder population, which is changed both by *artificial selection* for economic, cultural or aesthetic reasons,

inbreeding, by a *modified form of natural selection* in the human controlled environment, by *genetic drift*, and by *relaxation of natural selection* (Price, 1984, Clutton-Brock, 1999).

Artificial selection is unique to domestication and is the best understood mechanism. Artificial selection may be applied either consciously (intentionally) or unconsciously (inadvertently). Personal biases and preferences often influence the selection of breeding stock and these may be very subtle (Price, 1999).

The ‘fox farm experiment’ (in Russia) created a new domestic animal (from the wild silver fox) by continuously selecting for tameness. After 40 years of continuous selection in over 45,000 foxes a variety of changes had occurred including piebald colouring, drooping ears, curly tails and shortened snouts (Trut, 1999, Belyaev, 1969, Belyaev, 1979). This demonstrates that selecting for a single trait has wide ranging and unexpected affects on the behavioural and physiological characteristics of an animal (Dobney and Larson, 2006). Even though only a single trait was selected for, it is unlikely that the genes responsible for that specific trait caused the raft of changes observed. As it stands, only a few genes have been found that are responsible for morphological change in domesticates (e.g. MC1R and coat colour (Ludwig et al., 2009) and although it is possible that there is ‘master’ suit of genes for observed affects of domestication, untangling them is highly problematic (Dobney and Larson, 2006).

Inbreeding can be a problem in small closed populations resulting in a reduction of genotypic variability within a population as well as in "inbreeding depression",

which is the lowering of vigour or fitness brought about by the expression of many deleterious genes previously masked by dominant or epistatic alleles (Price, 1984).

Inbreeding has been practiced (combined with artificial selection) in order to obtain a particular characteristic (e.g., unusual morphological characteristics). Through systematic inbreeding a degree of homogeneity and constancy of characteristics that is normally not seen in wild populations can be achieved (Price, 1984, 1999). The loss of variability as the result of inbreeding is less costly to a population being maintained by humans, who often attempt to preserve variants that would normally not survive in nature. Early adopters of domestic populations must either have continuously 'drip-fed' in new wild animals to keep the genetic variability of their stock healthy, out-bred domestic females with wild males, had a large enough population to avoid the worst effects of inbreeding or had unhealthy animals. Inbreeding may be one major reason for failed domestication events.

Natural selection in captivity encompasses all the selection in captivity not ascribed to artificial selection. This depends on what the captive environment allows for development and expression of species-typical biological characteristics, and the number of generations in captivity (Price, 1999).

Once animals are in a human controlled environment the founder group is subjected to population bottlenecking that can result in intermittent and sometimes significant *genetic drift*. In small populations drift is likely to reduce variability within populations but increase it between populations (Clutton-Brock, 1999, Price, 1984).

Relaxation of natural selection occurs with the transition from the natural environment to the captive one. Behaviours that are strongly selected for in the wild lose their significance once captive e.g. the ability to find food and water. As a result the variability for these traits is likely to increase, reducing the population's fitness for survival in the wild (Price, 1999).

1.3.6 Changes seen in Domesticated Animals

The mechanisms of biological change associated with domestication are expressed through morphological variation and behavioural modification. For example body size reduction has often been noted in the early stages of domestication (Albarella, 2002, Clutton-Brock, 1988, Ervynck et al., 2001, Payne and Bull, 1988) although it is a poor marker of domestication due to the difficulty of determining the contribution of natural taxonomic, environmental and spatial variation to its occurrence (Zeder, 2006c).

One of the best catalogued differences between wild and domestic animals is the proposed paedomorphic changes of the skull. Paedomorphism is the retention of juvenile morphology or behaviour into adulthood, expressed in morphology as snout shortening and concavity of the face where the occipital squama becomes upturned, braincase reduction, hair softening and loss, tooth crowding and tooth length reduction combined with an overall reduction in body size (Bokonyi, 1974, Price, 1999, Zeder, 2012). Behavioural paedomorphism includes tameness, expressed as a lack of fear and increased inquisitiveness and social bonds with reduced aggression (Wayne, 1986, Coppinger et al., 1987, Trut et al., 2009, Hare et al., 2012).

Paedomorphism is caused by heterochronic changes (Price, 1999, Zeder, 2012, Alberch et al., 1979), the evolutionary process that generates diversity via changes in the rate or timing of ontogenetic pathways (Gould, 1977), and which has been directly attributed as the mechanism for the morphological change in dogs (Moray, 1992, Moray, 1994), and other domesticates (Trut, 1999, Zeder, 2012).

(Gould, 1977) described three components of ontogeny - age, size and shape. The evolutionary disassociation of these three components during ontogeny can produce descendent morphology that either resembles the ancestral morphology at a younger stage of development (paedomorphosis) or a continued stage of development (peramorphosis) (Alberch et al., 1979). Paedomorphism can arise from either the mechanisms of neoteny, slowing the growth rate of shape relative to age; progenesis, reducing the period of growth in shape, resulting in early sexual maturity; and post displacement, where shape growth occurs later (Godfrey and Sutherland, 1995). It is neoteny that is often invoked to explain the divergent morphology of domestic animals. However, closer examination of the cranial characteristics of dogs (Drake, 2011) have shown that they do not share the morphological characteristics of adult or juvenile wolves, and that the vast range of phylogenetically novel dog skull shapes does not coincide with the expectations of the heterochronic model. This leaves the model of morphological change uncertain.

An increase in variability of coat colour/change in pelage has been noted in animals around the Mesolithic/Neolithic transition (Clutton-Brock, 1999). Increasing coat colour variability has been linked to the MC1R gene (Anderson, 2007, Ludwig et al., 2009) with the suggestion that different coat colours in domesticates were artificially

selected for. An increase in variety of pelage characters, such as lengthening of the ears, long tails or more useful characteristics such as thicker wool/hair may also have been selectively breed, either for identification (from wild or other breeders stock) or as a desirable, usable characteristic (Clutton-Brock, 1999).

These changes could have appeared fast, slow or not at all according to the type of modification, the species and the strictness of the conditions imposed (Vigne et al., 2005, Vigne, 2011b). Arguments have been made that in many cases the process is slow (Arbuckle, 2005, Ervynck et al., 2001) as the early forms of domestic animals do not exhibit overt morphological change. But domestic animals not closely segregated from wild animals would have experienced continuous gene flow with the local wild populous, and as such were still linked with natural selective pressures whilst simultaneously experiencing reduced pressures from inbreeding and artificial selection. Yet morphological change can also happen extremely quickly, as witnessed in insular mammals (Millien et al., 2006), thus Vigne's suggestion that morphological change is dependent on context is probably correct.

In conclusion, some of the changes of domestication would initially have been an unintended consequence of the evolutionary/developmental mechanisms involved, while others were the result of artificial selection e.g. coat colour. Some of these modifications result from hormonal changes, due to environmental conditions and the stress of captivity, (i.e. without human intent (Arbuckle, 2005) whereas others result from epigenetic/developmental changes (heterochrony) or are purely genetic mutations possibly selected by humans (Vigne, 2011b).

1.3.7 Wild Progenitors

One of the major issues in the study of domestication is the identification of the wild ancestors of domestic species. This question has implications in finding the earliest sites of domestication, as wild animals must be present to be domesticated. Conversely, where animals appear outside their natural range there is a strong case for human interference and possible domestication (Rowley-Conwy 2011).

In the case of pigs it has been proposed that the eastern and western pigs were domesticated separately (Darwin, 1868). The earliest domestication events were in south-west Asia (Ervynck et al., 2001), with later centres in Europe and south-east Asia (Larson et al., 2007b). The European and South-West Asian progenitor is relatively easy to ascertain as only *Sus scrofa* inhabits it, but determining the exact subspecies is harder as *S.s. scrofa*, *S.s. attila* and *S.s. lybicus* are all present in this region, thus the exact subspecies is not known.

The Asian progenitor is harder to ascertain. Darwin attributed it to *Sus indicus*, which has since been split into various sub-species (Groves, 1981). There were also multiple domestication events in South East Asia (Larson et al., 2005, Larson et al., 2007b, Larson et al., 2010) and it seems probable that several species were domesticated at different times in different events, involving at least *S. scrofa*, *S.s. moupinensis*, *S.s. cristatus* on the continent and *S. scrofa* and *S. celebensis* in Island South East Asia (Groves, 1981, Larson et al., 2007b, Cucchi et al., 2011).

1.3.8 The Domestication of Pigs: When, Where and How Many Times?

When and where species were domesticated is an area of great interest (Vigne, 2011a). Although it is hard to pinpoint the exact moment of domestication due to the inexact nature of the methodologies (see below), and depends on the definition of domestication used, it is accepted that the region that the first domestic animals appear in is the Near East. Excluding dogs (which were domesticated much earlier than other animals) the earliest domesticates were sheep, goats, cows, pigs and cats from approximately the middle of the 11th millennium BP (Vigne, 2011a). Further separate domestication events from local stock also took place in the Zagros with goats at ca 10kys BP and cattle domestication in Pakistan (the Indus valley) (ca. 8.5 kys BP).

Genetic studies have shown that following the original pig domestication event(s) in the Near East, domestic pigs from there were introduced to Europe (from around 7,500 BP) (Larson et al., 2007a) as part of a proposed 'Neolithic package' (Childe, 1925, Childe, 1936, Vigne, 2011a, Rowley-Conwy, 2011). The suggested routes the introduction followed are around the coastline of the Mediterranean basin (Zeder, 2008) and through the Balkans and into central Europe, a possible route around the Black Sea is also possible. The progression of the Neolithic through Europe is shown below (Figure 6).

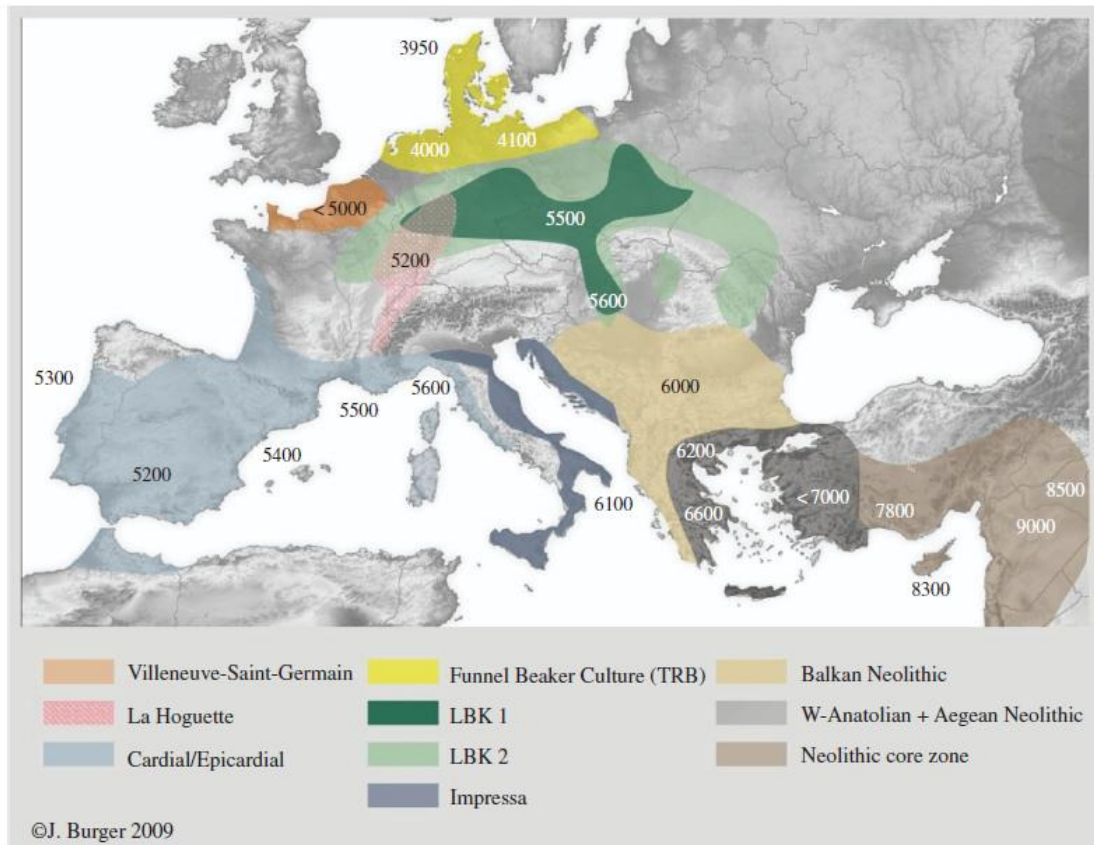


Figure 6: Arrival dates and approximate geographical expansions of defined Early Neolithic cultures from (Burger and Thomas, 2011)

The Near Eastern type pigs disappeared in mainland Europe by the Iron Age (2700 BP) and were replaced by indigenous pigs, suggesting introgression with the local populations (see figure 7). European pigs were subsequently exported back into the Near East. Multiple clades of domestic pigs indigenous to Europe (e.g. the separate Italian and Sardinian clade and the 2 mainland European lineages) provide evidence of additional localised domestication events (Larson *et al* 2007a).

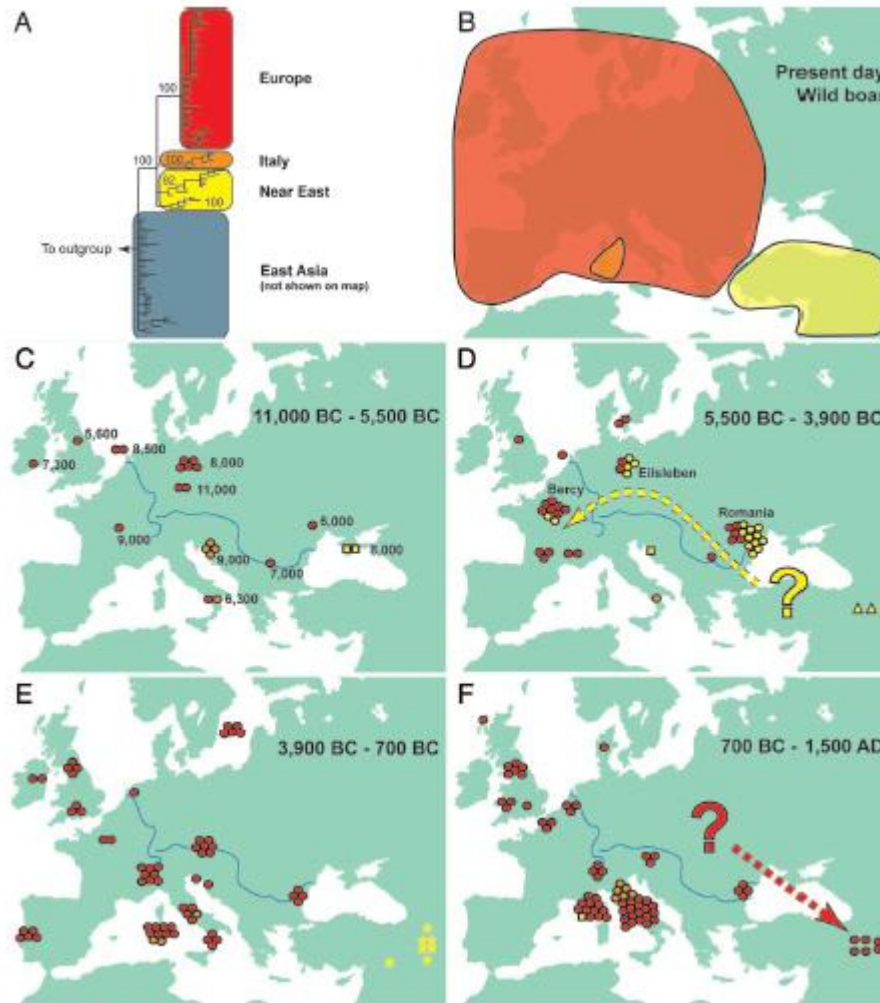


Figure 7: Series of Maps from (Larson et al., 2007b) depicting (A) the mitochondrial separation of European, Italian, Near Eastern and East Asia pigs, (B) the present distribution of the mitochondrial haplotypes, (C-F) the introduction and introgression of Near Eastern haplotype pigs into mainland Europe during the Neolithic and Bronze Age, with the following dispersal of European haplotype pigs into the Near East in the Iron Age.

Genetic studies (Larson et al., 2005) of pig mitochondria (thus based on the maternal lineage) initially established that there were at least 7 centres of domestication in the Near and Far East, this number has since been increased by 5, 1 in India, 3 in peninsular Southeast Asia and 1 of the coast of Taiwan (Larson et al., 2010). Domestication was occurring at different times and in different places, the lack of overlap in genetic (mitochondrial) signatures (Haplogroups) disproves any

suggestion of expansion or migration into these cases (unlike Europe). Thus it can be concluded that domestication was not an isolated or unusual event but was in fact quite a common phenomenon (Dobney and Larson, 2006).

1.3.9 The Study of Pig Domestication

Wild pigs were first formally described by Linnaeus (*Sus scrofa*) in 1758 and domestic pigs by Erxleben (*Sus scrofa domesticus*) in 1777 (Gentry et al., 2004). The effects of Domestication have been studied since Charles Darwin's seminal book 'On the origin of Species' (1859) included a chapter on human induced variation caused by domestication. He followed this up with a two volume work 'The variation of plants and animals under domestication' (1868). These applied his theories of natural selection to the morphological variation and inheritability of characters under the influence of domestication, and included a chapter on domestic pigs. It considered the wild progenitors of domestic pigs and their variability in the wild, including changes in the morphology of the skull and other morphological 'curiosities', convergence of characteristics in eastern and western pig 'races', changes in the length of gestation, shared characteristics in the coat colours of young pigs of all types and feral and cross-bred pigs.

1.3.10 Methods used in the Study of Pig Domestication

The earliest and most commonly used method to distinguish domestic pigs from wild pigs is size, the premise being that the earliest domestic pigs were smaller than their wild progenitors due to changes in diet, restricted range, relaxation of morphological characteristics associated with breeding success in the wild and population bottlenecks (and founder effect) with genetic drift (Zeder, 2006a).

The first formal methodology⁴ for detecting domestic pigs was devised by Ludwig Rüttimeyer (1860, 1864) focusing on the length of the tooth row and 3rd molars of pigs from an early Swiss Neolithic lakeside site. He concluded that there were 3 types of pigs present, wild, domestic and ‘peat’ (*Torfschwein*) pigs (*Sus scrofa palustris*) that were postulated to be the domestic descendents of Near Eastern stock pigs. These were separated on size, e.g. his *ferus* (wild) pig 3rd molars he placed in the size bracket 40-53mm long and the *palustris* in the 33-39mm bracket. This was a controversial finding at the time, criticism focusing on a lack of adequate comparative material and the confounding effect of sexual dimorphism (this was successfully rejected on the basis that male and female maxillae were present in both wild and domestic samples). Though the *S.s palustris* sample was later amalgamated with the domestic type pigs⁵ (Nehring, 1889, Rowley-Conwy et al., 2012) the definition of wild and domestic based on size differences was established. Since then size differences have been the basis of discrimination between wild and domestic pigs and other animals. Measurements have been formalised and standardised by von den Dreisch (1976) and assemblages made available for general comparative purposes (Albarella and Payne, 2005).

1.3.11 Methodological Issues

One of the obvious problems with size as a basis for determining the status between wild and domestic animals is that animal size varies for reasons other than domestication. Temperature and other environmental factors, diet and individual

⁴ Prior to this several Scandinavian naturalists has identified wild pigs through size on an ad-hoc basis, see Rowley-Conwy (2012:3-4).

⁵ Thus *S.s. palustris* is not a currently recognised sub-species (Groves 1981)

variation are all contributing factors to size changes (Zeder, 2006a). Climatic variation can be overcome by only comparing samples from similar habitats and temporal sequences (to eliminate climate change over time), but this can be very restrictive in availability of climatic data and suitable comparative material and excludes regional comparisons. Individual variation can be accounted for either by using larger samples, or by conflating measurements of different elements (cranial and post-cranial) using the log ratio method (Payne and Bull, 1988). The effects of diet on size and stature are not well documented but it is thought that teeth will be less affected as they are less plastic than bone (Cucchi et al., 2011).

Ontogenetic (age related) change can be mitigated to some degree by concentrating only on adults, pigs' remains may be aged by epiphyseal fusion, tooth eruption and tooth wear (Silver, 1969). However there are issues with these approaches, some bones continue to grow after fusion, teeth can be reduced in size due to the growth of other teeth e.g. 2nd molars can be worn down by the emergence of 3rd molars (Rowley-Conwy 2011) and the methodologies are based on modern proxy populations (Greenfield and Arnold, 2008).

Sexual dimorphism can be a major issue (Payne and Bull, 1988, Vigne et al., 2005), especially in goats where the use of body size as a domestic marker has been questioned (Zeder, 2001, Zeder, 2006a) on the basis that the most causal factor of size differentiation is sex and not wild/domestic status. One way around this is by assigning sex to individuals, but this can be problematic in analyses of post-cranial material or for other animals where sexing bones is difficult.

Another major methodological issue is detecting the presence of multiple, distinct populations. For example, in a sexually dimorphic animal assemblage where wild and domestic animals of both sexes are present there could potentially be four separate populations. Alternatively there could be 'semi-domesticated' or indeterminately wild/domestic animals (animals undergoing the domestication process) present (Jarman, 1971, 1976b). There are also potential issues of interbreeding (deliberate or otherwise) with contemporary wild individuals (Dwyer, 1996). To recognise multiple populations in the archaeological record (Payne and Bull, 1988) suggested using Pearson's co-efficient of variation (the standard deviation of a sample expressed as a percentage of its mean). This is a normalized measure of dispersion of a probability distribution, in this case the variation within the overall sample. Comparison with other assemblages allows discrimination between samples with only a single population (lower co-efficient of variation) and samples with multiple populations (large co-efficient of variation).

There are important repercussions from husbandry strategy on using size as a domestic marker. If animals were kept under loose supervision and allowed to interbreed with the local wild population the resultant free gene-flow between them would restrict any size change (Rowley-Conwy, 2011). Only if domestic animals were kept under strict segregation from wild animals is any morphological size change likely to occur in the domestic population. Thus size variation is only likely to recognise animals that conform to 'wild' or 'domestic' in the traditional sense, yet size can still be used to document domestication as in the early Euphrates valley, where there is a temporally deep archaeological record and gradual changes over time have been recorded (Peters et al., 2005). Thus traditional biometrical techniques

still have their place (Albarella, 2002) despite the associated issues. To gain a greater resolution other methodologies must be used in addition to size to spot any early transitional domestic animals, or domestic animals that were kept in alternative husbandry strategies.

1.3.12 Alternative Methodologies

Demographic profiling was one of the first non-morphological methods applied to studying domestication (Zeder, 2006b, Zeder, 2006a). This is based on the assumption that the age and sex of animals killed by hunters maximising their return will be different from those killed by herders interested in the long term viability of their herds. Thus domestic animals will be killed younger (with an emphasis on killing young males and keeping older females for breeding) as herders control and manage their slaughter strategies to maximise productivity (Rowley-Conwy et al., 2012).

Sex determination is based either on sexual dimorphism of size or other morphological characteristics. In pigs this is most often the shape of the canine (von den Driesch, 1976). Age at death data is taken from the epiphyseal fusion of post-cranial elements and tooth eruption and wear (Silver, 1969). Assemblages with large numbers of slaughtered young males and older females (typical of a traditional herding strategy) may be indicative of domestication, as suggested by (Zeder, 2001) for the early Zagros.

This method can be problematic in species, such as pigs, where sex determination is difficult, especially in juveniles, and in archaeological assemblages where bones are

often fragmentary. In animals with high natural fecundity (e.g. pigs) there is naturally a higher mortality rate (Oliver, 1993) which can ape the domestic mortality profile. Intensive hunting strategies may also lead to higher mortality of juveniles; thus distinguishing between intensive hunting, close herding or some intermediate stage may be hard (Rowley-Conwy et al., 2012), yet may reveal significant changes in subsistence strategies between periods.

Linear Enamel Hypoplasias (LEHs) are dental defects that are produced during moments of physiological stress in an animal's early life. If stress occurs during tooth development it can result in marked incremental lines and depressions (beyond those that naturally occur) in tooth enamel that are known as LEHs. Once the stress is resolved normal growth resumes, leaving the LEH as a permanent marker of the stress event (Dobney and Ervynck, 2000). As tooth formation is relatively predictable and regular it can be used to give clues as to the health of animals during their formative years. LEH are infrequent in wild and modern domestic populations, yet in early domestic populations LEH are sometimes more common, suggesting incidents of stress in early closely managed populations (Rowley-Conwy et al., 2012). While it can be hard to distinguish between wild and domestic levels of LEH or determine the level of those of pigs not closely supervised/feral/semi-domestic, an increasing proportion of LEHs in a population over time provides additional evidence of domestication.

Stable isotopes and diet can be used to differentiate between wild and domestic pigs, as the feeding of livestock has been described as a pre-condition of domestication (Price, 1984). Diets of tightly controlled domestic pigs should differ from those of

wild pigs, and even the diet of pigs loosely associated with humans should differ from that of wild pigs with little or no contact with humans as pigs scavenge for human dietary discards (Dwyer, 1996). Pigs are omnivorous (see 1.2.2) and can and will eat a highly varied diet; this would have been one of the factors making them attractive to early adopters of agriculture.

One way to determine differences in diet is to compare the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ scores of populations. Stable isotopes show a trophic level effect in which the relative proportions of one isotope change in a systematic way between food source and consumer. This change, called fractionation, depletes or enriches isotopes ratios, which is then compared to look for change (Ambrose, 1993, Reitz and Wing, 1999). High ^{13}C scores indicate the influence of C_4 plants in diets, as different photosynthetic pathways (e.g. C_3 vs. C_4 plants) discriminate differently against ^{13}C . Animals eating root crops, legumes, wheat (*Triticum aestivum*), rice (*Oryza sativa*), wild fruit, nuts and foliage have a $\delta^{13}\text{C}$ approaching those of C_3 plants. C_3 plants are more common than C_4 plants and have a lower $^{13}\text{C}/^{12}\text{C}$ ratio than C_4 plants. Animals eating C_4 plants, which include millet (*Panicum miliaceum*), sorghum (*Sorghum vulgare*) and tropical grasses (C_4 plants are more common in the tropics) have a higher $^{13}\text{C}/^{12}\text{C}$ ratio. Nitrogen ratios can also differ among plants, legumes fix Nitrogen through symbiotic bacteria, which source nitrogen from a combination of the soil and air. Air has a lower $\delta^{15}\text{N}$ value than soil so legumes have a lower $^{15}\text{N}/^{14}\text{N}$ ratio than plants that receive all their nitrogen from the soil. The marine environment has a higher $\delta^{15}\text{N}$ value than the terrestrial environment, and the bone collagen reflects this, with marine vertebrates showing a significantly higher $\delta^{15}\text{N}$ value than that of land vertebrates (van der Merwe et al., 1993). Together these

can be used to investigate the proportions of marine and C₄ plants in past population diets. In addition, bioaccumulation of the heavier isotopes through the food chain can be used to investigate trophic level, and the proportion that meat contributes to diet (Reitz and Wing, 1999).

Carbon and nitrogen stable isotopes of pig bones from the sites in Western Asia, Europe, East Asia (China and Japan) confirm that there are significant dietary differences between wild boars and domestic pigs. The $\delta^{15}\text{N}$ values of domestic pigs from Neolithic sites in Southeast Anatolia, Turkey were lower than those of wild boars because of large quantity of pulse in their diets (Lösch et al., 2006). The domestic pigs in Ryukyu Islands, Japan, had higher $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ values than wild boars in other islands, owing to different feeding patterns by humans (Matsui et al., 2005, Minagawa et al., 2005). In early northern China, Shandong Province, three distinct populations of pigs were found, A group with low $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, B group with high $\delta^{13}\text{C}$ and intermediate $\delta^{15}\text{N}$ values and C group with low $\delta^{13}\text{C}$ and high $\delta^{15}\text{N}$ values. In comparison with the stable isotope values of humans, wild boars and domestic pigs during Yangshao Culture and Longshan Culture, A group was attributed to wild boars while B and C group belonged to domesticated pigs (Hu et al., 2008).

The field of *genetics* has made a huge impact on the studies of domestication. As discussed above one aim has been to identify the origins and numbers of domestication events. Once the identification of the biogeographic distribution of wild animal haplotypes is complete the presence of domestic individuals within them can point to a domestication event. Movement of different haplogroups can be used

as an indication of the spread of domestication, as in (Larson et al., 2007a) study of the spread of domestic pigs in Europe (see section 1.3.8). Issues with this approach remain in species with little biogeographic structure (Hofreiter et al., 2004), such as dogs, and there are issues with ancient DNA preservation (Dobney and Larson, 2006, Campos et al., 2012), but this approach has granted insights to human migrations and early domestication in chickens (Gongora et al., 2008, Storey et al., 2008) and cows (Edwards et al., 2007).

The possibility of discovering genes responsible for the expression of traits associated with domestication has been postulated (Stricklin, 2001) yet finding a complete suite of domestication genes is unlikely due to the complex interactions of genes, and genes the environment (Dobney and Larson, 2006, Anderson, 2007). There has been some success identifying individual genes associated with domestication, such as the MC1R gene that regulates the expression of pelage colouring (Anderson, 2007). An increase in the diversity of colour (especially the emergence of piebald colouring) is associated with domestication in all domestic animals (Darwin, 1868). MC1R has been used to study the domestication of horses (Ludwig et al., 2009), an increase in the diversity of coat colour suggests that horses were domesticated around 4,500BC in Kazakhstan.

Geometric morphometric methods (GMM) have recently gained traction in the field of domestication studies in pigs and horses. Geometric morphometrics is the study of morphology using a suit of powerful statistical tools to examine variation in the morphology of bones or teeth such as those caused by the environment or by human influence (i.e. domestication). The application of this methodology in

zooarchaeology has focused on teeth, as mammalian teeth do not vary much due to environmental factors, instead being genetically controlled. Teeth also survive particularly well in the archaeological record and with GMM most teeth can be analysed. Tooth shape studies have been used to identify some of the earliest domestic pigs in China (Cucchi et al., 2011). Phenetic relationships here revealed clear phenotypic signatures in samples of modern and Neolithic pigs; which provided evidence for pig domestication at the site of Jiahu from at least 6600 BC cal., establishing the Yellow River region as one of the earliest centres of independent Chinese pig domestication. Studies of animals from Island South East Asia (Cucchi et al., 2009) suggested that wild pigs on New Guinea were the descendants of pigs domesticated in mainland South East Asia and introduced by early farmers to ISEA although there was no clear evidence for a Neolithic introduction of domesticated pigs, or for the local domestication of indigenous bearded pigs.

GMM has also been applied to post-cranial material. Analysis of horse metapodials in early human hunting sites in North and South Western Europe during the Late Glacial showed strong regional structuring of horse populations (Bignon et al., 2005), suggesting an absence of long distance migrations and the fragmentation of populations. This is consistent with postulated mosaic landscapes of the “Mammoth-Steppe” biome that occurred during the Late Glacial in Eurasia and confirms the existence of early complex and diversified hunting communities. Analysis of Cervid anatomy associated with locomotion has been applied to palaeo-climatic reconstruction of the plio-pleistocene (Curran, 2012), using adaptations of animals to open or closed environments to determine what climate existed where their remains were recovered.

Bibliography

- ALBARELLA, U. 2002. *Size matters: how and why biometry is still important in zooarchaeology*, Oxford, Oxbow Books.
- ALBARELLA, U., DOBNEY, K., ERVYNCK, A. & ROWLEY-CONWY, P. 2007. Introduction. In: ALBARELLA, U., DOBNEY, K., ERVYNCK, A. & ROWLEY-CONWY, P. (eds.) *Pigs and Humans: 10,000 Years of Interaction*. Oxford: Oxford University Press.
- ALBARELLA, U., DOBNEY, K. & ROWLEY-CONWY, P. 2006a. *The Domestication of the Pig (Sus scrofa) New Challenges and Approaches*.
- ALBARELLA, U., DOBNEY, K. & ROWLEY-CONWY, P. 2009. Size and shape of the Eurasian wild boar (*Sus scrofa*), with a view to the reconstruction of its Holocene history. *Environmental Archaeology*, 14, 103-136.
- ALBARELLA, U., MANCONI, F., ROWLEY-CONWY, P. & VIGNE, J.-D. 2006b. Pigs of Corsica and Sardinia: A biometrical re-evaluation of their status and history. In: TECCHIATI, U. & SALA, B. (eds.) *Archaeozoological studies in honour of Alfredo Riedel*. Province of Bolzano: Bolzano.
- ALBARELLA, U. & PAYNE, S. 2005. Neolithic pigs from Durrington Walls, Wiltshire, England: a biometrical database. *Journal of Archaeological Science*, 32, 589-599.
- ALBERCH, P., GOULD, S. J., OSTER, G. F. & WAKE, D. B. 1979. Size And Shape In Ontogeny And Phylogeny. *Paleobiology*, 5, 296-317.
- AMBROSE, S. H. 1993. Isotopic analysis of palaeodiets: methodological and interpretive considerations. In: SANDFORD, K. M. (ed.) *Investigations of ancient human tissue: chemical analysis in anthropology*. Philadelphia: Gordon and Breech Science Publishers.
- ANDERSON, L. 2007. The Molecular Basis for Phenotypic Changes During Pig Domestication. In: ALBARELLA, U., DOBNEY, K., ERVYNCK, A. & ROWLEY-CONWY, P. (eds.) *Pigs and Humans: 10,000 Years of Interaction*. Oxford: Oxbow Books.
- ARBUCKLE, B. S. 2005. *Experimental Animal Domestication and its Application to the Study of Animal Exploitation in Prehistory*, Oxford, Oxbow Books.
- BELLWOOD, P. 2005. *First Farmers: The Origins of Agricultural Societies*, Oxford, Blackwell Publishing.
- BELYAEV, D. K. 1969. Domestication Of Animals. *Science Journal*, 5, 47-&.
- BELYAEV, D. K. 1979. Destabilizing Selection As A Factor In Domestication. *Journal of Heredity*, 70, 301-308.
- BIGNON, O., BAYLAC, M., VIGNE, J. D. & EISENMANN, W. 2005. Geometric morphometrics and the population diversity of Late Glacial horses in Western Europe (*Equus caballus arcelini*): phylogeographic and anthropological implications. *Journal of Archaeological Science*, 32, 375-391.
- BOKONYI, S. 1974. *History of Domestic Mammals in Central and Eastern Europe*, Budapest, Akademiai Kiado.
- BURGER, J. & THOMAS, M. G. 2011. The palaeopopulation genetics of humans, cattle and dairying in Neolithic Europe. In: PINHASI, R. & STOCK, J. (eds.) *The bioarchaeology of the transition to agriculture*. Chichester: Wiley Blackwell.

- BURTON, J. & MACDONALD, A. A. 2010. *Sus celebensis*: IUCN Red List of Threatened Species [Online]. Available: www.iucnredlist.org.
- CALDECOTT, J. O., BLOUCH, R. A. & MACDONALD, A. A. 1993. The Bearded pig (*Sus barbatus*). In: OLIVER, W. (ed.) *Pigs, Peccaries, and Hippos: Status Survey and Conservation Action Plan*. Gland, Switzerland: IUCN.
- CAMPOS, P. F., CRAIG, O. E., TURNER-WALKER, G., PEACOCK, E., WILLERSLEV, E. & GILBERT, M. T. P. 2012. DNA in ancient bone - where is it located and how should we extract it? *Annals of anatomy = Anatomischer Anzeiger : official organ of the Anatomische Gesellschaft*, 194, 7-16.
- CHILDE, V. G. 1925. *The Dawn of European Civilization*, London, Routledge & Kegan Ltd.
- CHILDE, V. G. 1936. *Man Makes Himself*, London, Watts.
- CLUTTON-BROCK, J. 1988. *The Walking Larder: Patterns of Domestication, Pastoralism and Predation*, London/Boston, Unwin Hyman.
- CLUTTON-BROCK, J. 1999. *A Natural History of Domesticated Animals*, Cambridge, Cambridge University Press.
- COPPINGER, R., GLENDINNING, J., TOROP, E., MATTHAY, C., SUTHERLAND, M. & SMITH, C. 1987. Degree of Behavioral Neoteny Differentiates Canid Polymorphs. *Ethology*, 75, 89-108.
- CROCKFORD, S. 2002. Animal domestication and heterochronic speciation: the role of thyroid hormone. In: MINUGH-PURVIS, N. & MCNAMARA, K. (eds.) *Human Evolution Through Developmental Change*. Baltimore: Johns Hopkins University Press.
- CROCKFORD, S. 2006. *Rhythms of Life: Thyroid Hormone and the Origin of Species*. Bloomington. USA. Trafford Publishing
- CUCCHI, T., FUJITA, M. & DOBNEY, K. 2009. New Insights into Pig Taxonomy, Domestication and Human Dispersal in Island South East Asia: Molar Shape Analysis of *Sus* Remains from Niah Caves, Sarawak. *International Journal of Osteoarchaeology* 19, 508-530.
- CUCCHI, T., HULME-BEAMAN, A., YUAN, J. & DOBNEY, K. 2011. Early Neolithic pig domestication at Jiahu, Henan Province, China: clues from molar shape analyses using geometric morphometric approaches. *Journal of Archaeological Science*, 38, 11-22.
- CURRAN, S. C. 2012. Expanding ecomorphological methods: geometric morphometric analysis of Cervidae post-crania. *Journal of Archaeological Science*, 39, 1172-1182.
- DARWIN, C. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, London, John Murray.
- DARWIN, C. 1868. *The Variation of Animals and Plants Under Domestication* London, John Murray.
- DAVIS, S. J. M. 1981. The Effects of Temperature Change and Domestication on the Body Size of Late Pleistocene to Holocene Mammals of Israel. *Paleobiology*, 7, 101-114.
- D'HART, J. P., BUTYNSKI, T. M. & DE JONG, Y. 2008. *Phacochoerus aethiopicus* [Online]. IUCN. Available: www.iucnredlist.org.
- DOBNEY, K. & ERVYNCK, A. 2000. Interpreting developmental stress in archaeological pigs: The chronology of linear enamel hypoplasia. *Journal of Archaeological Science*, 27, 597-607.

- DOBNEY, K. & LARSON, G. 2006. Genetics and animal domestication: new windows on an elusive process. *Journal of Zoology*, 269, 261-271.
- DRAKE, A. G. 2011. Dispelling dog dogma: an investigation of heterochrony in dogs using 3D geometric morphometric analysis of skull shape. *Evolution & Development*, 13, 204-213.
- DWYER, P. D. 1996. Boars, barrows, and breeders: The reproductive status of domestic pig populations in mainland New Guinea. *Journal of Anthropological Research*, 52, 481-500.
- EDWARDS, C. J., BOLLONGINO, R., SCHEU, A., CHAMBERLAIN, A., TRESSET, A., VIGNE, J. D., BAIRD, J. F., LARSON, G., HO, S. Y. W., HEUPINK, T. H., SHAPIRO, B., FREEMAN, A. R., THOMAS, M. G., ARBOGAST, R. M., ARNDT, B., BARTOSIEWICZ, L., BENECKE, N., BUDJA, M., CHAIX, L., CHOYKE, A. M., COQUEUGNIOT, E., DOHLE, H. J., GOLDNER, H., HARTZ, S., HELMER, D., HERZIG, B., HONGO, H., MASHKOUR, M., OZDOGAN, M., PUCHER, E., ROTH, G., SCHADELINDIG, S., SCHMOLCKE, U., SCHULTING, R. J., STEPHAN, E., UERPMANN, H. P., VOROS, I., VOYTEK, B., BRADLEY, D. G. & BURGER, J. 2007. Mitochondrial DNA analysis shows a Near Eastern Neolithic origin for domestic cattle and no indication of domestication of European aurochs. *Proceedings of the Royal Society B-Biological Sciences*, 274, 1377-1385.
- ENDO, H., HAYASHI, Y., YAMAZAKI, K., MOTOKAWA, M., PEI, J.-C. K., LIN, L.-K., CHOU, C.-H. & OSHIDA, T. 2002. Geographical Variation of Mandible Size and Shape in the Wild Pig (*Sus scrofa*) from Taiwan and Japan. *Zoological Studies*, 41, 452-460.
- ERVYNCK, A., DOBNEY, K., HONGO, H. & MEADOW, R. 2001. Born Free? New Evidence for the Status of *Sus scrofa* at Neolithic Çayönü Tepesi (Southeastern Anatolia, Turkey). *Paléorient* 27, 47-73.
- ESTES, R. 1991. *The Behavior Guide to African Mammals, Including Hoofed Mammals, Carnivores, Primates*, Los Angeles, University of California Press.
- EVERSHED, R. P., PAYNE, S., SHERRATT, A. G., COPLEY, M. S., COOLIDGE, J., UREM-KOTSU, D., KOTSAKIS, K., OZDOGAN, M., OZDOGAN, A. E., NIEUWENHUYSE, O., AKKERMANS, P. M., BAILEY, D., ANDEESCU, R. R., CAMPBELL, S., FARID, S., HODDER, I., YALMAN, N., OZBASARAN, M., BICAKCI, E., GARFINKEL, Y., LEVY, T. & BURTON, M. M. 2008. Earliest date for milk use in the Near East and southeastern Europe linked to cattle herding. *Nature*, 455, 528-31.
- FANG, M. & ANDERSSON, L. 2006. Mitochondrial diversity in European and Chinese pigs is consistent with population expansions that occurred prior to domestication. *Proceedings of the Royal Society B: Biological Sciences*, 273, 1803-1810.
- FINLAYSON, C. 2004. *Neanderthals and Modern Humans: An Ecological and Evolutionary Perspective*, Cambridge Cambridge University Press.
- FOREIGN AGRICULTURAL SERVICE (FAS), U. S. D. O. A. 2012. *Production, Supply and Distribution Online* [Online]. Available: <http://www.fas.usda.gov/psdonline/psdQuery.aspx>
- FUNK, S. M., VERMA, S. K., LARSON, G., PRASAD, K., SINGH, L., NARAYAN, G. & FA, J. E. 2007. The pygmy hog is a unique genus: 19th

- century taxonomists got it right first time round. *Molecular Phylogenetics and Evolution*, 45, 427-436.
- GALTON, F. 1865. The First Steps Towards the Domestication of Animals. *Transactions Ethnological Society London*. In: DENT, J. M. (ed.) *Inquiries into Human Faculty*. London.
- GAUTIER, A. 1990. *La Domestication. Et l'Homme Créé ses Animaux.* , Paris, Errance.
- GENOV, P. V. 1999. A Review of the Cranial Characteristics of the Wild Boar (*Sus scrofa* Linnaeus 1758), with Systematic Conclusions. *Mammal Review*, 29, 205-238.
- GENTRY, A., CLUTTON-BROCK, J. & GROVES, C. 2004. The naming of wild animal species and their domestic derivatives. *Journal of Archaeological Science*, 31, 645-651.
- GODFREY, L. R. & SUTHERLAND, M. R. 1995. Whats Growth Got To Do With It - Process And Product In The Evolution Of Ontogeny. *Journal of Human Evolution*, 29, 405-431.
- GONGORA, J., CUDDAHEE, R. E., NASCIMENTO, F. F. D., PALGRAVE, C. J., LOWDEN, S., HO, S. Y. W., SIMOND, D., DAMAYANTI, C. S., WHITE, D. J., TAY, W. T., RANDI, E., KLINGEL, H., RODRIGUES-ZARATE, C. J., ALLEN, K., MORAN, C. & LARSON, G. 2011. Rethinking the evolution of extant sub-Saharan African suids (Suidae, Artiodactyla). *Zoologica Scripta*, 40, 327-335.
- GONGORA, J., RAWLENCE, N. J., MOBEGI, V. A., JIANLIN, H., ALCALDE, J. A., MATUS, J. T., HANOTTE, O., MORAN, C., AUSTIN, J. J., ULM, S., ANDERSON, A. J., LARSON, G. & COOPER, A. 2008. Indo-European and Asian origins for Chilean and Pacific chickens revealed by mtDNA. *Proceedings of the National Academy of Sciences*, 105, 10308-10313.
- GOULD, S. J. 1977. *Ontogeny and Phylogeny*, Cambridge MA, The Belknap Press of Harvard University Press.
- GREENFIELD, H. J. & ARNOLD, E. R. 2008. Absolute age and tooth eruption and wear sequences in sheep and goat: determining age-at-death in zooarchaeology using a modern control sample. *Journal of Archaeological Science*, 35, 836-849.
- GROVES, C. 1981. *Ancestors for the Pigs: Taxonomy and Phylogeny of the Genus Sus*, Canberra, Research School of Pacific Studies, Australian National University.
- GROVES, C. 1997. Taxonomy of wild pigs (*Sus*) of the Philippines. *Zoological Journal of the Linnean Society*, 120, 163-191.
- GROVES, C. 2001. Mammals in Sulawesi: Where did they come from and when, and what happened to them when they got there? . In: METCALFE, I., SMITH, J. M. B., MORWOOD, M. & DAVIDSON, I. (eds.) *Faunal and Floral Migration and Evolution in SE Asia-Australasia*. Lisse, The Netherlands: A.A. Balkema Publishers.
- GROVES, C. 2007. Current views on taxonomy and zoogeography of the genus *Sus*. In: ALBARELLA, U., DOBNEY, K. & ROWLEY-CONWY, P. (eds.) *Pigs and Humans: 10,000 years of interaction*. Oxford: Oxford University Press.
- GROVES, C. & SCHALLER, G. B. 2000. The Phylogeny and Biogeography of the Newly Discovered Annamite Artiodactyls. In: VRBA, E. S. & SCHALLER, G. B. (eds.) *Antelopes, Deer and Relatives: Fossil Record, Behavioral*

- Ecology, Systematics and Conservation*. New Haven and London: Yale University Press.
- GRUBB, P. 1993a. *Eurasian Suids Sus and Babyrousa*., Cornell University, IUCN.
- GRUBB, P. 1993b. *The Afrotropical Suids Phacochoeris, Hylochoerus and Potamochoerus: taxonomy and distribution*. , Cornell University, IUCN.
- GUPPY, N. 1961. *Wai-Wai Through the Forests North of the Amazon*, London, Penguin Books.
- HAFEZ, E. S. E. 1968. *Adaption of Domestic Animals*, Philadelphia, Lea & Febiger.
- HAMPTON, O. W. 1999. *Culture of stone: sacred and profane uses of stone among the Dani*, Texas Texas A&M University Press
- HARE, B., WOBBER, V. & WRANGHAM, R. 2012. The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, 83, 573-585.
- HARRIS, M. 1974. *Cows, Pigs, Wars & Witches*, Glasgow, William Collins Sons & Co.
- HIGGS, E. S. & JARMAN, M. R. 1972. The Origins of Animal and Plant Husbandry. In: HIGGS, E. S. (ed.) *Papers in Economic Prehistory*. Cambridge: Cambridge University Press.
- HOFREITER, M., SERRE, D., ROHLAND, N., RABEDER, G., NAGEL, D., CONARD, N., MÜNZEL, S. & PÄÄBO, S. 2004. Lack of phylogeography in European mammals before the last glaciation. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 12963-12968.
- HONGO, H., ISHINGURO, N., WATANOBE, T., SHIGEHARA, N., ANEZAKI, T. & LONG, V. T. 2002. Variation in mitochondrial DNA of Vietnamese pigs: relationships with Asian domestic pigs and Ryukyu wild boars. *Zoologica Science*, 19, 1329-1335.
- HU, Y., LUAN, F., WANG, S., WANG, C. & RICHARDS, M. 2008. Preliminary attempt to distinguish the domesticated pigs from wild boars by the methods of carbon and nitrogen stable isotope analysis. *Science in China Series D: Earth Sciences*, 52, 85-92.
- INGOLD, T. 1994. From trust to domination: an alternative history of human-animal relations. . In: MANNING, A. & SERPELL, J. (eds.) *Animals and human society: changing perspectives* London and New York. : Routeledge.
- JARMAN, M. 1971. Culture and economy in the North Italian Neolithic. *World Archaeology*, 2.
- JARMAN, M. R. 1976a. Early animal husbandry. *Philosophical Transactions of the Royal Society of London B* 275, 85-97.
- JARMAN, M. R. 1976b. Prehistoric economic development in sub-Alpine Italy. In: DE SIEVEKING, G., LONGWORTH, I. H. & WILSON, K. E. (eds.) *Problems in economic and social archaeology*. London: Duckworth.
- KAWANISHI, K., GUMAL, M. & OLIVER, W. 2010. *Sus barbatus*: IUCN Red List of Threatened Species [Online]. Available: www.iucnredlist.org.
- KIJAS, J. M. H. & ANDERSON, L. 2001. Phylogenetic study of the origin of the domestic pig estimated from the near-complete mtDNA genome. *Journal of Molecular Evolution*, 52, 302-308.
- KIM, K. I., LEE, J. H., LI, K., ZHANG, Y.-P., GONGORA, J. & MORAN, C. 2002. Phylogenetic relationships of Asian and European pig breeds determined by mitochondrial DNA D-loop sequence polymorphism. *Animal Genetics* 33, 19-25.

- LARSON, G., ALBARELLA, U., DOBNEY, K., ROWLEY-CONWY, P., SCHIBLER, J., TRESSET, A., VIGNE, J. D., EDWARDS, C. J., SCHLUMBAUM, A., DINU, A., BALACSESCU, A., DOLMAN, G., TAGLIACCOZZO, A., MANASERYAN, N., MIRACLE, P., VAN WIJNGAARDEN-BAKKER, L., MASSETI, M., BRADLEY, D. G. & COOPER, A. 2007a. Ancient DNA, pig domestication, and the spread of the Neolithic into Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 15276-15281.
- LARSON, G., CUCCHI, T., FUJITA, M., MATISOO-SMITH, E., ROBINS, J., ANDERSON, A., ROLETT, B., SPRIGGS, M., DOLMAN, G., KIM, T. H., THUY, N. T. D., RANDI, E., DOHERTY, M., DUE, R. A., BOLLT, R., DJUBIANTONO, T., GRIFFIN, B., INTOH, M., KEANE, E., KIRCH, P., LI, K. T., MORWOOD, M., PEDRINA, L. M., PIPER, P. J., RABETT, R. J., SHOOTER, P., VAN DEN BERGH, G., WEST, E., WICKLER, S., YUAN, J., COOPER, A. & DOBNEY, K. 2007b. Phylogeny and ancient DNA of *Sus* provides insights into neolithic expansion in island southeast Asia and Oceania. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 4834-4839.
- LARSON, G., DOBNEY, K., ALBARELLA, U., FANG, M. Y., MATISOO-SMITH, E., ROBINS, J., LOWDEN, S., FINLAYSON, H., BRAND, T., WILLERSLEV, E., ROWLEY-CONWY, P., ANDERSSON, L. & COOPER, A. 2005. Worldwide phylogeography of wild boar reveals multiple centers of pig domestication. *Science*, 307, 1618-1621.
- LARSON, G., LIU, R., ZHAO, X., YUAN, J., FULLER, D., BARTON, L., DOBNEY, K., FAN, Q., GU, Z., LIU, X.-H., LUO, Y., LV, P., ANDERSSON, L. & LI, N. 2010. Patterns of East Asian pig domestication, migration, and turnover revealed by modern and ancient DNA. *Proceedings of the National Academy of Sciences*, 107, 7686-7691.
- LINNAEUS, K. 1740. *Systema naturæ in quo naturæ regna tria, secundum classes, ordines, genera, species, systematice proponuntur*, Stockholm.
- LINNAEUS, K. 1758. *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis.*, Stockholm.
- LUCCHINI, V., MEIJAARD, E., DIONG, C. H., GROVES, C. P. & RANDI, E. 2005. New phylogenetic perspectives among species of South-east Asian wild pig (*Sus* sp.) based on mtDNA sequences and morphometric data. *Journal of Zoology*, 266, 25-35.
- LUDWIG, A., PRUVOST, M., REISSMANN, M., BENECKE, N., BROCKMANN, G. A., CASTANOS, P., CIESLAK, M., LIPPOLD, S., LLORENTE, L., MALASPINAS, A.-S., SLATKIN, M. & HOFREITER, M. 2009. Coat Color Variation at the Beginning of Horse Domestication. *Science*, 324, 485-485.
- LÖSCH, S., GRUPE, G. & PETERS, J. 2006. Stable Isotopes and Dietary Adaptations in Humans and Animals at Pre-Pottery Neolithic Nevalı Cori, Southeast Anatolia. *American Journal of Physical Anthropology* 131, 181-193.
- MACDONALD, A. A. 2010a. *Babyrussa babyrussa*: IUCN Red List of Threatened Species [Online]. Available: www.iucnredlist.org.
- MACDONALD, A. A. 2010b. *Babyrussa celebensis*: IUCN Red List of Threatened Species [Online]. Available: www.iucnredlist.org.

- MACDONALD, A. A. 2010c. *Babyroura togeanensis*: IUCN Red List of Threatened Species [Online]. Available: www.iucnredlist.org.
- MASSEI, G. & GENOV, P. V. 2004. The Environmental Impact of Wild Boar. *Galemys*, 16, 135-145.
- MATSUI, A., ISHINGURO, N., HONGO, H. & MINAGAWA, M. 2005. Wild pig? Or domesticated boar? An archaeological view on the domestication of *Sus scrofa* in Japan. In: VIGNE, J. D., PETERS, J. & HELMER, D. (eds.) *The First Steps of Animal Domestication: New Archaeological Approaches*. Oxford: Oxbow Books.
- MCCORMICK, F. & MURRAY, E. 2007. *Knowth and the zooarchaeology of Early Christian Ireland (Excavations at Knowth 3)*, Dublin, Royal Irish Academy.
- MCDONALD-BROWN, L. 2009. *Choosing and Keeping Pigs: A Complete Practical Guide*, London, Gaia Books.
- MEADOW, R. 1989. Osteological evidence for the process of animal domestication. In: CLUTTON-BROCK, J. (ed.) *The Walking Larder: Patterns of domestication, pastoralism and predation*. London: Unwin-Hyman.
- MEIJAARD, E. & GROVES, C. 2002a. Proposal for taxonomic changes within the genus *Babyroura*. *IUCN/SSC Pigs, Peccaries, and Hippos Specialist Group (PPHSG) Newsletter* 2, 9-10.
- MEIJAARD, E. & GROVES, C. 2002b. Upgrading three subspecies of *Babirusa* (*Babyroura* sp.) to full species level. *Asian Wild Pig News: Asian wild pig Research and Conservation group*, 2, 33-39.
- MEIRI, S., RAIA, P. & PHILLIMORE, A. B. 2011. Slaying dragons: limited evidence for unusual body size evolution on islands. *Journal of Biogeography*, 38, 89-100.
- MILLIEN, V., KATHLEEN LYONS, S., OLSON, L., SMITH, F. A., WILSON, A. B. & YOM-TOV, Y. 2006. Ecotypic variation in the context of global climate change: revisiting the rules. *Ecology Letters*, 9, 853-869.
- MINAGAWA, M., MATSUI, A., ISHINGURO, N. & HONGO, H. 2005. Patterns of prehistoric boar *Sus scrofa* domestication, and inter-islands pig trading across the East China Sea, as determined by carbon and nitrogen isotope analysis. *Chemical Geology*, 218, 91-102.
- MITTEROECKER, P., GUNZ, P. & BOOKSTEIN, F. L. 2005. Heterochrony and geometric morphometrics: a comparison of cranial growth in *Pan paniscus* versus *Pan troglodytes*. *Evolution & Development*, 7, 244-258.
- MORAY, D. F. 1992. Size, shape, and development in the evolution of the domestic dog. *Journal of Archaeological Science*, 19, 181-204.
- MORAY, D. F. 1994. The early evolution of the domestic dog. *American Scientist*, 82, 336-347.
- NEHRING, A. 1889. Über Torfschwein und Torfrind. *Verhandlungen der Berliner Gesellschaft für Anthropologie, Ethnologie und Urgeschichte*, 363-369.
- OLIVER, W. 1993. *Pigs, Peccaries and Hippos*, Gland Switzerland, IUCN.
- OLIVER, W. 2010a. *Sus ahoenobarbus*: IUCN Red List of Threatened Species [Online]. Available: www.iucnredlist.org.
- OLIVER, W. 2010b. *Sus cebifrons*: IUCN Red List of Threatened Species [Online]. Available: www.iucnredlist.org.
- OLIVER, W. & HEANEY, L. 2010. *Sus philippensis*: IUCN Red List of Threatened Species [Online]. Available: www.iucnredlist.org.
- OLIVER, W. & LEUS, K. 2008. *Sus scrofa* [Online]. IUCN. Available: www.iucnredlist.org [Accessed 2/21/2012 2012].

- ORLIAC, M. J., PIERRE-OLIVIER, A. & DUCROCQ, S. 2010. Phylogenetic relationships of the Suidae (Mammalia, Cetartiodactyla): new insights on the relationships within Suoidea. *Zoologica Scripta*, 39, 315-330.
- PARKER-PEARSON, M. 1999. Food, Sex and Death: Cosmologies in the British Iron Age with Particular Reference to East Yorkshire. *Cambridge Archaeological Journal*, 9, 43-69.
- PAYNE, S. & BULL, G. 1988. Components of variation in measurements of pig bones and teeth, and the use of measurements to distinguish wild from domestic pig remains. *Archaeozoologia*, 2, 27-65.
- PETERS, J., VON DEN DRIESCH, A. & HELMER, D. 2005. The upper Euphrates-Tigris basin: Cradle of agropastoralism? In: VIGNE, J. D., PETERS, J. & HELMER, D. (eds.) *First Steps of Animal Domestication. New Archaeozoological Approaches*. Oxford: Oxbow Books.
- PHILLIPS, S. 2007. The pig in medieval iconography. In: ALBARELLA, U., DOBNEY, K., ERVYNCK, A. & ROWLEY-CONWY, P. (eds.) *Pigs and Humans: 10,000 Years of Interaction*. Oxford: Oxford University Press.
- POLLY, P. D. & ERONEN, J. T. 2011. Chapter 15 - Mammal Associations in the Pleistocene of Britain: Implications of Ecological Niche Modelling and a Method for Reconstructing Palaeoclimate. In: ASHTON, N. & CHRIS, S. (eds.) *Developments in Quaternary Sciences*. Elsevier.
- PRICE, E. O. 1984. Behavioral-Aspects Of Animal Domestication. *Quarterly Review of Biology*, 59, 1-32.
- PRICE, E. O. 1999. Behavioral development in animals undergoing domestication. *Applied Animal Behaviour Science*, 65, 245-271.
- PRUMMEL, W., HALICI, H. & VERBAAS, A. 2011. The bone and antler tools from the Wijnaldum-Tjitsma terp. *Journal of Archaeology in the Low Countries*, 3.
- QUEROUIL, S. & LEUS, K. 2008. *Potamochoerus porcus* [Online]. IUCN Available: www.iucnredlist.org.
- READING, R. W. 2005. Breaking the mold: a consideration of variation in the evolution of animal domestication. In: VIGNE, J. D., HELMER, D. & PETERS, J. (eds.) *The first steps of animal domestication: new archaeozoological approaches*. Oxford: Oxbow Books.
- REITZ, E. & WING, E. 1999. *Zooarchaeology*, Cambridge, Cambridge University Press.
- RINDOS, D. 1980. Symbiosis, Instability, and the Origins and Spread of Agriculture: A New Model. *Current Anthropology*, 21, 751-772.
- ROOK, L. & MARTINEZ-NAVARRO, B. 2010. Villafranchian: The long story of a Plio-Pleistocene European large mammal biochronologic unit. *Quaternary International*, 219, 134-144.
- ROWLEY-CONWY, P. 2011. Westward Ho! The Spread of Agriculture from Central Europe to the Atlantic. *Current Anthropology*, 52, S431-S451.
- ROWLEY-CONWY, P., ALBARELLA, U. & DOBNEY, K. 2012. Distinguishing Wild Boar from Domestic Pigs in Prehistory: A Review of Approaches and Recent Results. *Journal of World Prehistory*, 25, 1-44.
- ROWLEY-CONWY, P., HALSTEAD, P. & COLLINS, P. 2002. Derivation and application of a Food Utility Index (FUI) for European wild boar (*Sus scrofa* L.). *Environmental Archaeology* 7, 77-87.

- ROWLEY-CONWY, P. & LAYTON, R. 2011. Foraging and farming as niche construction: stable and unstable adaptations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, 849-862.
- RUTIMEYER, L. 1860. Untersuchung der Tierreste aus den Pfahlbauten der Schweiz. *Mitteilungen der Antiquarischen Gesellschaft in Zurich*, 13 (part 2, section 2), 31-72.
- RUTIMEYER, L. 1864. Neue Beiträge zur Kenntnis des Torfscheins. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 4, 139-186.
- SACK, W. O. 1982. *Essentials of Pig Anatomy: Horowitz/Kramer Atlas of Musculoskeletal Anatomy of the Pig*, Ithaca, New York, Veterinary Textbooks.
- SCANDURA, M., IACOLINA, L. & APOLLONIO, M. 2011. Genetic diversity in the European wild boar *Sus scrofa*: phylogeography, population structure and wild x domestic hybridization. *Mammal Review*, 41, 125-137.
- SCANDURA, M., IACOLINA, L., CRESTANELLO, B., PECCHIOLI, E., DI BENEDETTO, M. F., RUSSO, V., DAVOLI, R., APOLLONIO, M. & BERTORELLE, G. 2008. Ancient vs. recent processes as factors shaping the genetic variation of the European wild boar: are the effects of the last glaciation still detectable? *Molecular Ecology*, 17, 1745-1762.
- SEYDACK, A. 2008. *Potamochoerus larvatus* [Online]. IUCN. Available: www.iucnredlist.org.
- SILVER, I. A. 1969. The ageing of domestic animals. In: BROTHWELL, D. & HIGGS, E. S. (eds.) *Science in Archaeology*. London: Thames and Hudson.
- SOMMER, R. S. & NADACHOWSKI, A. 2006. Glacial refugia of mammals in Europe: evidence from fossil records. *Mammal Review*, 36, 251-265.
- STOREY, A. A., QUIROZ, D., RAMÍREZ, J. M., BEAVAN-ATHFIELD, N., ADDISON, D. J., WALTER, R., HUNT, T., ATHENS, J. S., HUYNEN, L. & MATISOO-SMITH, E. A. 2008. Pre-Columbian chickens, dates, isotopes, and mtDNA. *Proceedings of the National Academy of Sciences*, 105, E99.
- STRICKLIN, W. R. 2001. The evolution and domestication of social behaviour. In: KEELING, L. J. & GONYOU, H. W. (eds.) *Social behaviour in farm animals*. New York: CABI Publishing.
- TRUT, L. N. 1999. Early canid domestication: The farm-fox experiment. *American Scientist*, 87, 160-169.
- TRUT, L. N., OSKINA, I. & KHARLAMOVA, A. 2009. Animal evolution during domestication: the domesticated fox as a model. *Bioessays*, 31, 349-360.
- UZAL, A. & NORES, C. 2004. Endogenous and Exogenous constraints in the population changes of Wild Boar (*Sus scrofa* Linnaeus, 1758). *Galemys*, 16, 83-98.
- VAN DER MERWE, N. J., LEE-THORP, J. A. & RAYMOND, J. S. 1993. Light, stable isotopes and the subsistence base of formative cultures at Valdivia, Ecuador. In: LAMBERT, J. B. & GRUPE, G. (eds.) *Prehistoric human bone: archaeology at the molecular level*. Berlin: Springer Verlag.
- VERCAMMEN, P., SEYDACK, A. & OLIVER, W. 1993. The bush pigs (*Potamochoerus porcus* and *P. larvatus*). In: OLIVER, W. (ed.) *In Pigs, Peccaries and Hippos: Status Survey and Action Plan*. Gland, Switzerland: IUCN.
- VIGNE, J.-D., HELMER, D. & PETERS, J. 2005. New archaeological approaches to trace the first steps of animal domestication: general presentation, reflections and proposals. In: VIGNE, J. D., PETERS, J. & HELMER, D. (eds.) *First*

- Steps of Animal Domestication: New Archaeological Approaches*. Oxford: Oxbow Books.
- VIGNE, J.-D., ZAZZO, A., SALIÈGE, J.-F., POPLIN, F., GUILAINE, J. & SIMMONS, A. 2009. Pre-Neolithic wild boar management and introduction to Cyprus more than 11,400 years ago. *Proceedings of the National Academy of Sciences*, 106, 16135-16138.
- VIGNE, J. D. 2011a. The origins of animal domestication and husbandry: A major change in the history of humanity and the biosphere. *Comptes Rendus Biologies*, 334, 171-181.
- VIGNE, J. D. 2011b. The origins of animal domestication and husbandry: A major change in the history of humanity and the biosphere. *Comptes Rendus Biologies*, 334, 171-181.
- VON DEN DRIESCH, A. 1976. *A Guide to the Measurement of Animal Bones from Archaeological Sites*, Cambridge, MA, Peabody Museum Bulletin 1.
- WAYNE, R. K. 1986. Cranial Morphology Of Domestic And Wild Canids - The Influence Of Development On Morphological Change. *Evolution*, 40, 243-261.
- WEINSTOCK, J. 2000. *Late Pleistocene reindeer populations in Middle and Western Europe. An Osteometrical Study of Rangifer Tarandus*, Tübingen, Mo Vince Verlag.
- ZEDER, M. 2012. Pathways to Animal Domestication. In: GEPTS, P., FAMULA, T. R., BETTINGER, R. L., BRUSH, S. B., DAMANIA, A. B., MCGUIRE, P. E. & QUALSET, C. O. (eds.) *Biodiversity in Agriculture: Domestication, Evolution, and Sustainability*. Cambridge: Cambridge University Press.
- ZEDER, M. A. 2001. A metrical analysis of a collection of modern goats (*Capra hircus aegargus* and *Capra hircus hircus*) from Iran and Iraq: implications for the study of caprine domestication. *Journal of Archaeological Science*, 28, 61-79.
- ZEDER, M. A. 2005. A view from the Zagros: new perspectives on livestock domestication in the Fertile Crescent. In: VIGNE, J. D., PETERS, J. & HELMER, D. (eds.) *First Steps of Animal Domestication. New Archaeozoological Approaches*. Oxford: Oxbow Books.
- ZEDER, M. A. 2006a. A Critical Assessment of Markers of Initial Domestication in Goats (*Capra hircus*). In: ZEDER, M.A., BRADLEY, D.G., EMSHWILLER, E., & SMITH, B.D., (eds.) *Documenting Domestication: New Genetic and Archaeological Paradigms*. Berkeley, Los Angeles, London: University of California Press.
- ZEDER, M. A. 2006b. Archaeological Approaches to Documenting Animal Domestication. In: ZEDER, M.A., BRADLEY, D.G., EMSHWILLER, E., & SMITH, B.D., (eds.) *Documenting Domestication: New Genetic and Archaeological Paradigms*. Berkeley, Los Angeles, London: University of California Press.
- ZEDER, M. A. 2006c. Central Questions in the Domestication of Plants and Animals. *Evolutionary Anthropology*, 15, 105-117.
- ZEDER, M. A. 2008. Domestication and early agriculture in the Mediterranean Basin: Origins, diffusion, and impact. *Proceedings of the National Academy of Sciences*, 105, 11597-11604.
- ZEDER, M. A. 2009. The Neolithic Macro-(R)evolution: Macroevolutionary Theory and the Study of Culture Change. *Journal of Archaeological Research*, 17, 1-63.

ZEUNER, F. E. 1963. *A History of Domestic Animals*, London, Hutchinson & Co.

Chapter 2 - Methodology

2.1 Material

This section gives details of the material that the thesis is based upon. First is a description of the object of the thesis – the pig cranium. This is followed by the numbers and origins of the samples included, as well as details of the institutions from which they were sampled. Then the particulars of the geographic and environmental covariates, including latitude, longitude, precipitation, temperature and elevation of the samples (used in the analysis of manuscript 2), and the methods used to age individuals of uncertain birth and/or death dates, including discussion of some of the associated issues. Finally, the problems with traditional methodologies that have been used previously to investigate some of the areas addressed by this thesis are detailed.

2.1.1 The suid cranium (from Sack (1982) and Sisson and Grossman (1910))

The head and neck of the pig resemble a cone with the apex at the snout and with the base blending into the body via a short neck. One of the dominant features of the suid cranium is the broad and prominent nuchal crest which is the highest part of the skull (see Figure 8a & c). It forms a part of the occipital bone, which thins laterally and turns downwards to form part of the temporal crest. The temporal crest is posterior to the centre of the nuchal crest, forming a concave depression that is flatter in domestic pigs than wild (Figure 8c). At the base of this depression sits the foramen magnum with two divergent ridges above it (Figure 8a: label A). The paramastoid processes are very long and straight, with the hypoglossal foramen either medial or posterior to the root of paramastoid (8b).

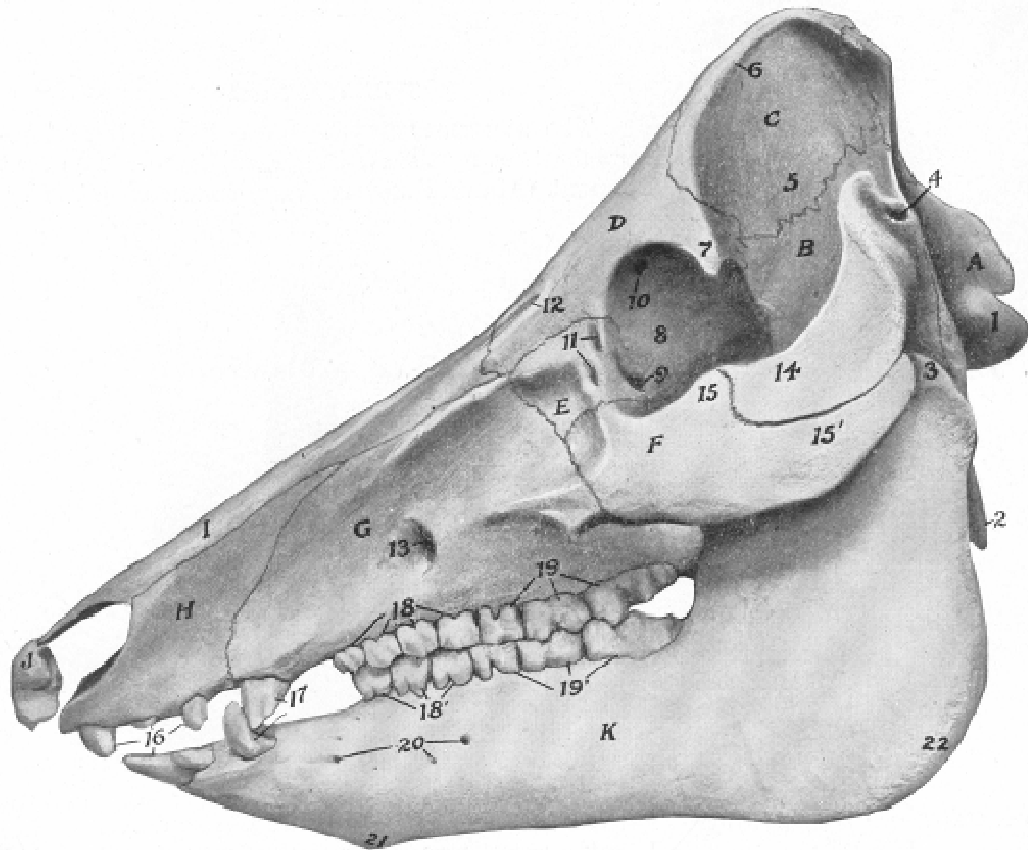


FIG. 177.—SKULL OF PIG; LATERAL VIEW.

A, Occipital bone; B, squamous temporal bone; C, parietal bone; D, frontal bone; E, lacrimal bone; F, malar bone; G, maxilla; H, premaxilla; I, nasal bone; J, os rostri; K, mandible; 1, occipital condyle; 2, paramastoid process; 3, condyle of mandible; 4, mentus acusticus externus; 5, temporal fossa; 6, parietal crest; 7, supraorbital process; 8, orbital part of frontal bone; 9, fossa for origin of ventral oblique muscle of eyeball; 10, orbital opening of supraorbital canal; 11, lacrimal foramina; 12, supraorbital foramen and groove; 13, infraorbital foramen; 14, zygomatic process of temporal bone; 15, temporal, and 15', zygomatic process of malar bone; 16, incisor teeth; 17, canine teeth; 18, 18', premolars; 19, 19', molars; 20, mental foramina; 21, mental prominence; 22, angle of mandible.

Figure 8a: Lateral view of a domestic pig skull (Sisson and Grossman, 1910)

The dorsal part of the skull is concave in domesticates, but flat in wild and feral animals, this concavity is produced by the frontal region becoming more vertical and a shortening of the nasal region. The nasal region consists of the nasal, frontal and parietal bones (8a: I, D, C) that are bounded on either side by the premaxilla, maxilla, the lacrimal and the squamous temporal bone (8a: H, G, C). The zygomatic arch is prominent, yet short, and bends upright at its posterior end (Figure 8a: 14 & 15). It consists of the malar (8a: F) and part of the temporal. At the tip of the snout is the rostral bone (8a: J) which is attached to the incisive part of the premaxilla and nasal. It forms the base of the hyper mobile disc-like movable tip of the snout and is used

extensively in its rooting behaviours. It is through this disc that the very long nasal cavity opens. The orbits are small and the rear of the orbit is open, as the supraorbital process (Figure 8a: 7) does not connect to the zygomatic.

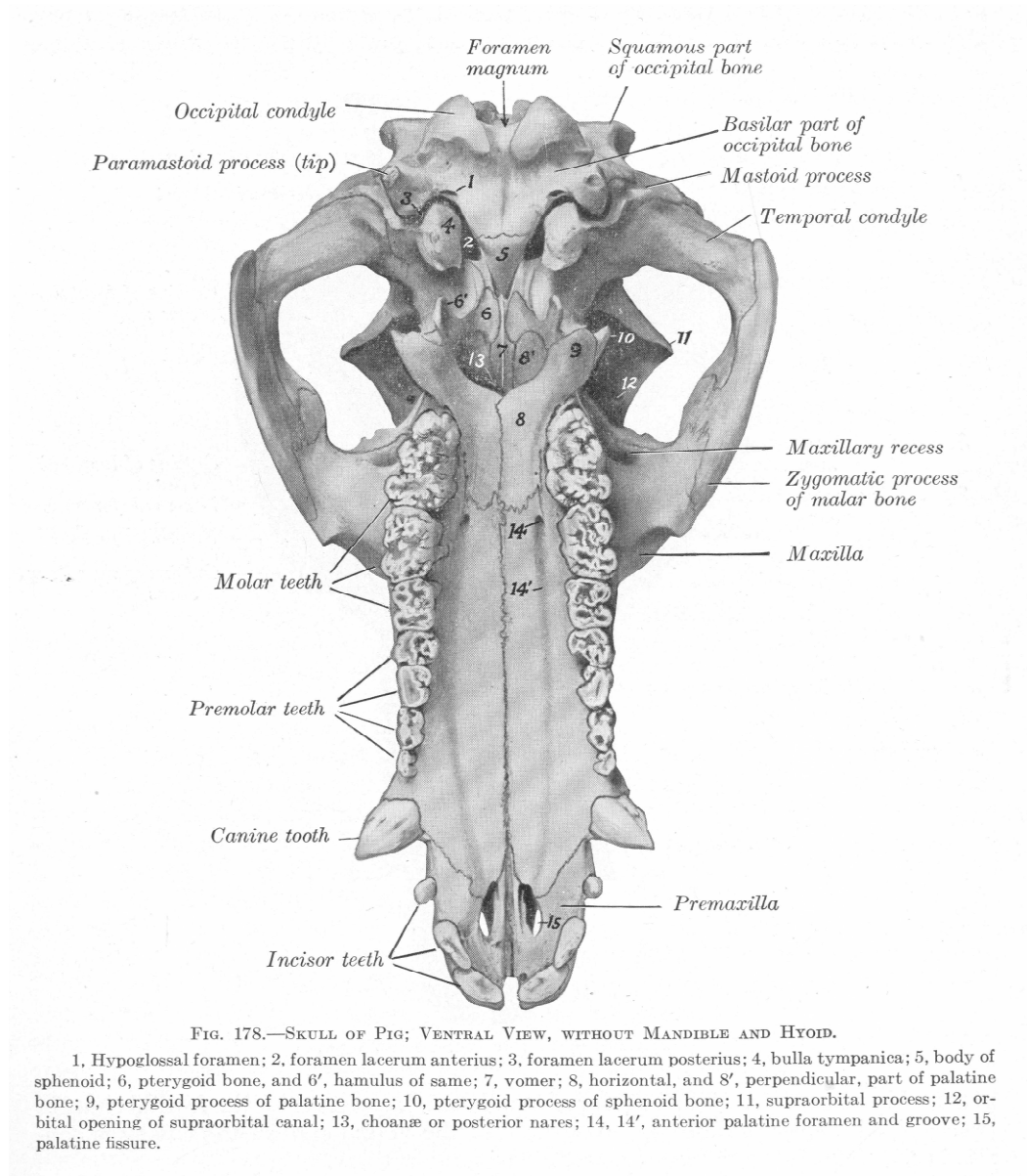


Figure 8b: basicranium of domestic pig crania (Sisson and Grossman, 1910)

The basicranium is split between the palate, containing the teeth, the maxilla and premaxilla (Figure 8b); and the main body of the cranium containing the bulla tympanica (8b:4), the posterior nares of the nasal aperture (8b:13), the palatine bone which includes the pterygoid process (8b:8), the basal part of the occipital (8b: 11 &

12), the root of the paramastoid (8b: 3) and a deep cavity containing the hyoid (8b: 2). The palate consists of the front two thirds of the cranium and is narrower in wild pigs than domestics; it widens at the molars and narrows at both ends. The dental formula of pigs is 3-1-4-3, with long straight lower incisors and curved upper incisors which allow a grasping action. The canines are the only obvious sexually dimorphic characteristic of pigs, and are much larger in males with a grooved channel on the interior surface of the female's lower canine. The canine root does not close and continues to grow throughout the pigs' life, the lower canine rubs against the upper canine, a constant sharpening action that allows the canine to be used in self-defence. The upper canine curves upwards, and in male *Babirusa* has spectacularly rotated through 180 degrees at the alveolus to form one of the most distinctive suid cranial characteristics (Sack, 1982, Sisson and Grossman, 1910, Groves, 1981).

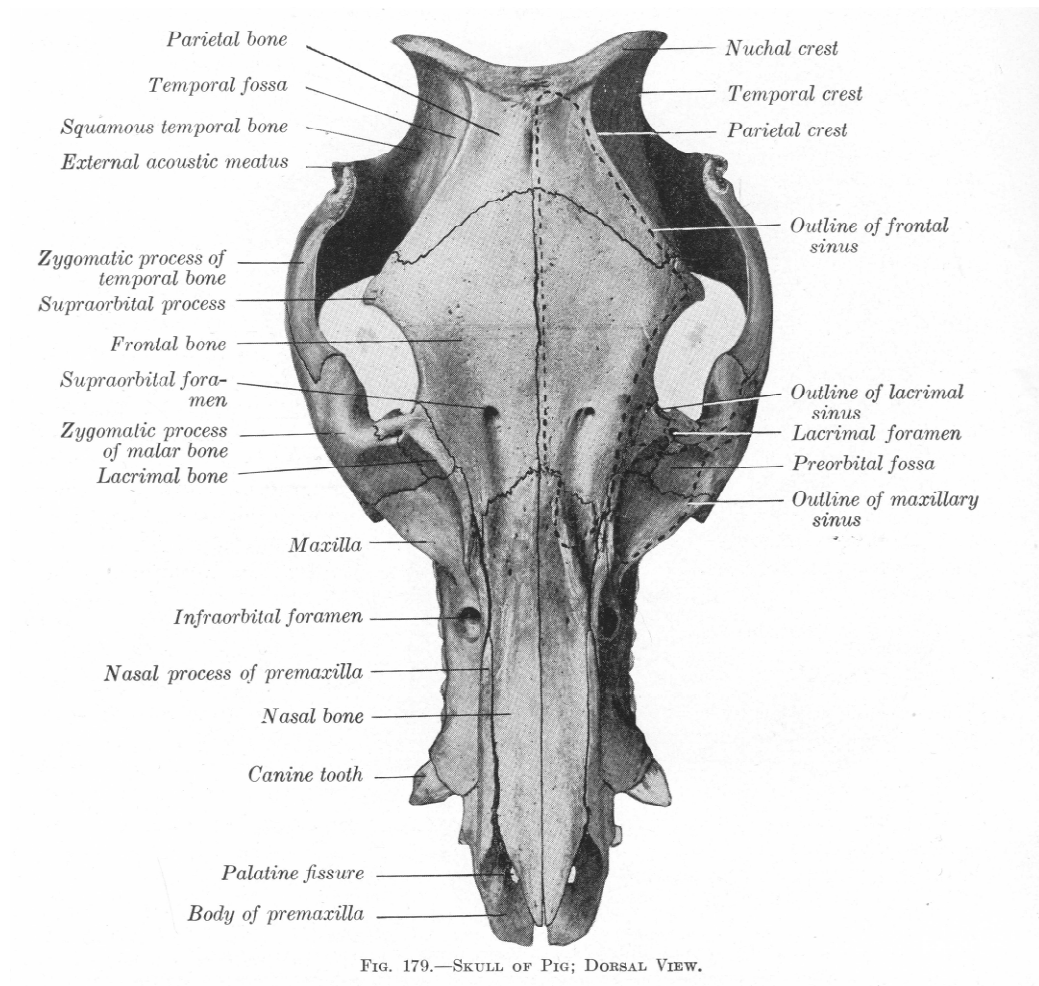


Figure 8c: Dorsal view of a domestic pig crania (Sisson and Grossman, 1910)

2.1.2 Materials

The data for this thesis come from several museum collections: the Museum für Naturkunde Berlin; the Natural History Museum, London; the Muséum National d'Histoire Naturelle, Paris; the Muséum d'Histoire Naturelle de la Ville de Genève; the Museum für Haustierkunde, Halle; the Field Museum of Natural History, Chicago; the American Museum of Natural History, New York; the Smithsonian National Museum of Natural History, Washington DC and the Royal (Dick) School of Veterinary Studies, Edinburgh.

Three-dimensional landmarks were collected from 1027 pig hemicrania (right side) - including all 3 sub-families of Suinae; the Babyrousini (*Babyrousa*), the Phacocherini (*Phacochoerus*) and especially the Suini (*Sus*), which forms the focus of this thesis.

For the family Phacocherinae 12 individuals of the genus *Ph.aethiopicus* were digitised. In the family Suidae examples from *Babyrousa*, *Potamochoerus* and *Sus* were digitised. Twenty-eight babirusa (family *Babyrousa*) were collected, mainly *B.celebensis* (22) but also *B.togeanensis* (6). Twenty-four *Potamochoerus*: 15 *P.larvatus* and 9 *P.porcus* were also included (see table 1, Manuscript 1 for details).

The sub-family Suinae is formed of 7 main species (see section 1.2.1) of which 6 are represented in this dataset: *S.barbatus* (32), *S.ahoenobarbus* (6), *S.cebifrons* (14), *S.celebensis* (45), *S.philippensis* (34) and *S.scrofa* (838 including domestics). The only major omission is *Sus verrucosus*, the Javan warty pig, for which no intact crania were available in any of the collections visited (see Table 1, Manuscript 2).

Sus scrofa is the most prolific of the *Sus* species, endemic to most of Eurasia, North-Africa and Island South-East Asia. Examples were collected from a wide variety of this range (see Figure 9), although no groups of a statistically significant size were collected from the Iberian Peninsula, South-East Europe or Central Russia. Future work would make adding these localities a priority. Domestic *Sus scrofa* were collected from the Museum fur Haustierkunde, Halle. The domestic breeds were Berkshire, Cornwall, Tamworth, Veredeltes Landschwein, Hannover-Braunschweig Landschwein and Deutsches Edelschwein, as well as a small sample of first

generation Tamworth-Wild pig hybrids (domestic sows and wild boars). See Manuscripts 3 & 4 for further details.

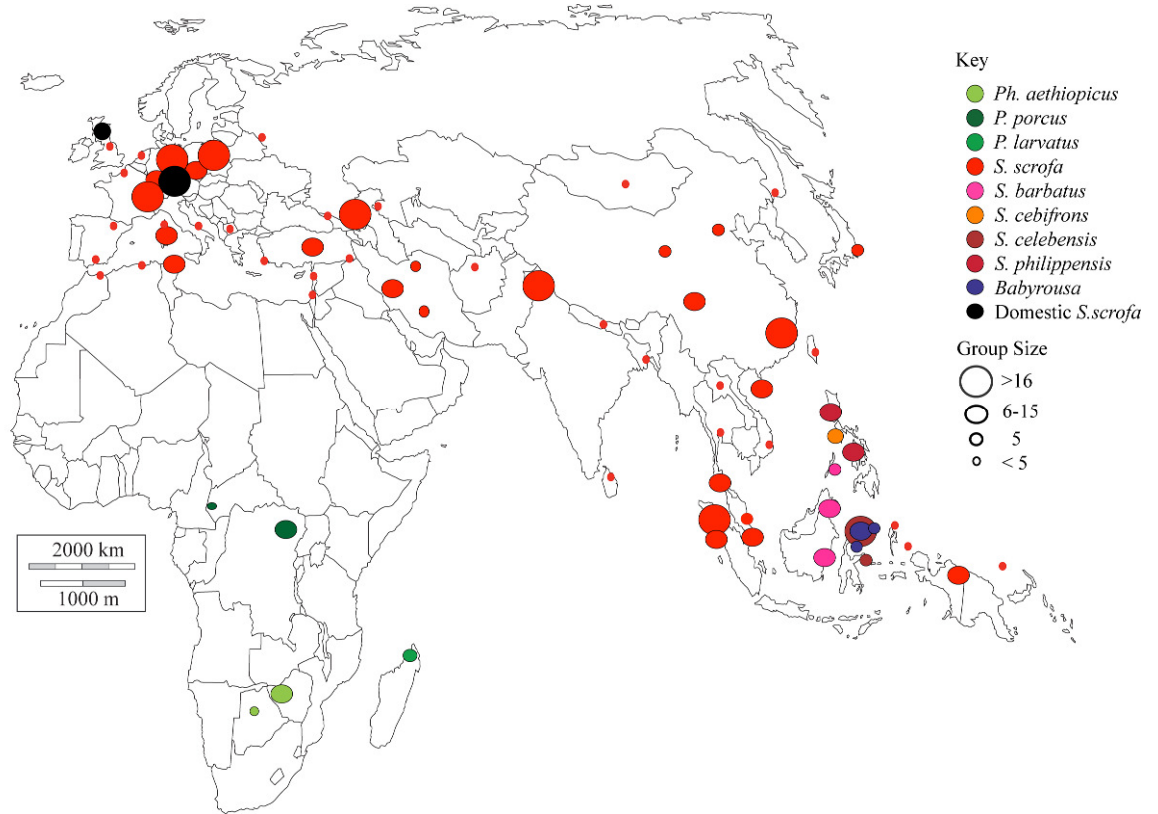


Figure 9: Distribution of samples

2.1.3 Covariates

Geographic covariates were derived from information in museum records; in many cases records were old and/or incomplete as the detail depended on the memory of the hunters or collectors. As a result the exact geographic origins for many of the samples are not known; consequently the data has been collated into geographic regions.

Temperature and precipitation data were extrapolated from the Wilmot and Matsura database (Legates and Willmott, 1990a, 1990b, Willmott and Feddema, 1992,

Willmott and Matsuura, 2001). Values were used for the mean group latitude and longitude. Elevation information for geographic co-ordinates originates from the SRTM3 database, a NASA global survey taken from the GPS visualiser website (Schneider, 2012).

2.1.4 Ageing methods

The majority of domestic individuals are of known age, with specific birth and death dates recorded at the Museum für Haüstierkunde Halle, Germany where they were reared.

It is not possible to assign absolute age of death for archaeological or wild specimens; instead they are assigned to age classes. Wild and domestic individuals of unknown birth or death dates were aged according to Higham (1967). This method is based on dental development, namely tooth eruption with older individuals aged by tooth wear. Tooth wear and eruption are common methods for ageing individuals within archaeological assemblages (Reitz and Wing, 1999) and are based on the premise that tooth eruption is predictable and occurs at the same stage of ontogeny in all individuals.

Problems exist with these methods, mainly a disconnection between proposed tooth eruption and wear classes with the absolute age of death, as variation with e.g. diet can have a profound impact of the rate top tooth wear (Greenfield and Arnold, 2008). There is also debate whether to base the age classes on absolute age of death data based on modern (Payne, 1973) or 19th century (Silver, 1969) pigs. Assessment of these forms of methodology have shown that tooth eruption is more accurate than

tooth wear, but both give broadly accurate estimates (Greenfield and Arnold, 2008, Jones, 2006). These methods are appropriate for this thesis as fine graded distinction is unnecessary between the broad natal, juvenile or adult classes used in manuscript 4.

2.1.5 Biometrics, and issues associated with them

Pigs in an archaeological context are traditionally recorded and compared using weight and size measures, including linear measurements. Traditional biometrics have been used to measure lengths, widths and depths of skeletal elements. Each measurement gives the magnitude of a dimension which is intrinsically size as well as shape based, and it is hard to separate the two components. They also do not give any information on the interior geometry of a shape and each measurement is generally treated individually, rather than as part of a single homologous shape. Additionally, measurements with similar start points are not independent, and if they run in the same direction they may duplicate information (Adams et al., 2004, O'Higgins, 2000, Slice, 2005, Zelditch et al., 2004).

In recent literature discussion has moved on to how biometrical methods may better explore shape. Albarella (2002) suggests that shape is an important tool in classical zooarchaeological studies. Investigations into issues with weight, gender and breed are all more likely to be answered through shape studies rather than size studies. The use of decimal log ratios (introduced into archaeology by Meadow (1981, 1999) and used by Payne and Bull (1988)) where populations of animals can be compared along the same axis (i.e. lengths or widths) to a standard animal form is suggested. This is a step up in complexity but still suffers from the same problems that all biometric

methods do (see above). Subsequently size change has been deemed to be an unsatisfactory method for demonstrating domestication events (Vigne *et al* 2005). As a result there has been a move to alternative research and methodologies, such as Eigenshape outline analysis on teeth – used to distinguish between wild and domestic individuals (Warman, 2005) which drawing from many of the same branches of statistics as geometric morphometrics; genetics (Zeder *et al* 2006), dental defects, such as linear enamel hypoplasia to reconstruct and contrast health of early wild and domestic populations (Dobney and Ervynck (2000); or demographic profiling to show the difference in subsistence strategies between hunter-gatherers and early pastoralists (Zeder, 2006).

2.2 Methods

This section initially explains the theory of Geometric Morphometrics, which underpins all the analyses conducted in this thesis, and is followed by a section containing an overview of the traditional multivariate statistical methods used to analyse the data further.

2.2.1 Geometric morphometrics

Geometric morphometrics is a suite of statistical techniques for the multivariate statistical analysis of Cartesian coordinate data. The data are usually represented by two or three dimensional landmark point locations, through which the information about the relative spatial arrangements of the landmarks is preserved throughout an analysis (Slice et al., 1996). The landmark points create a configuration that represents the biological structure under consideration - in this case, the pig cranium. The landmarks are specifically chosen to be homologous, to be relevant to the scientific questions being posed, and to represent the anatomical shape of the specimens according to set criteria (see 2.2.7). The configurations of landmarks are standardised through a superimposition method called Generalised Procrustes Analysis, from where they may be subjected to traditional multivariate statistics for data exploration and analysis.

2.2.2 Generalised Procrustes Analysis

The superimposition method used in this thesis, and most commonly used in GMM, is called Generalised Procrustes Analysis (GPA). This procedure consists of several steps. First, the configurations are centred on the mean configuration of all landmark co-ordinates, called the centroid (Bookstein, 1996a). Next the configuration is scaled

to the centroid by dividing each co-ordinate of each landmark by the centroid size of the configuration - the centroid size is the square root of the sum of squared distances of a set of landmarks to the centroid (Slice et al., 1996). Finally the configuration is rotated, beginning by aligning all specimens to the first shape of the configuration. This is achieved by minimising the squared distances between corresponding landmarks of the configurations (Gower, 1975). Once all configurations have been aligned to the first, the average shape is determined; all configurations are then rotated to this reference shape. This is repeated until the newly computed average shape ceases to change. Thus the final reference shape is the one that minimises the average distances of all the shapes in the configuration from itself.

After superimposition, shape differences can be described by the differences in coordinates of corresponding landmarks between objects. These differences can also be used as data in multivariate comparisons of shape variation (Bookstein, 1996a).

The process of rotation, translation and scaling creates a shape space where several dimensions are lost. This can be calculated as $pk - k - k(k - 1)/2 - 1$, where p is the number of landmarks and k is the number of dimensions. For three dimensional analysis this works out as $3p - 3 - 3 - 1$ which can be resolved as $3p - 7$ (Slice, 2005). This shape space is known as Kendall's shape space, so called having been first described by him as all the geometric information that remains once location, scale and rotational effects are filtered out from an object (Kendall, 1977, 1984). Thus GPA is the process of moving from a pre-shape space to a shape space – a space where shape is the differential between configurations of points (Zelditch et

al., 2004). GPA fitting was conducted in either Morphologika2 (O'Higgins and Jones, 2006) or MorphoJ (Klingenberg, 2008), and used in all Manuscripts.

2.2.3 Kendall's shape space and tangent space

Kendall's shape space has several properties that have significant implications with regard to geometric morphometrics. The first is that Kendall's shape space describes shape in a curved (non-Euclidean) space (Slice, 2001). Most statistical tools assume analysis is conducted in a Euclidean (linear) space (Mitteroecker and Gunz, 2009, Rohlf, 1998). This problem can be overcome either by working within Kendall's shape space and restricting the suite of useable statistics, or by projecting the coordinates from Kendall's shape space into a Euclidean space tangent to Kendall's shape space (Rohlf, 1996). This is an orthogonal projection from the GPA to a linear space tangent at the sample mean (Bookstein, 1996b) that preserves the distances between specimens within the two spaces (Slice, 2005). All GMM analysis in this thesis is conducted in such a tangent (Euclidean) space. The software tpsSmall (Rohlf, 1997) can be used to assess the accuracy of the approximation of the tangent space. In the case of this thesis, the approximation is good, and errors due to the differences in shape space should therefore be negligible.

The second relevant property is that independent isotropic distributions (invariant with respect to direction) of landmarks result in isotropic distributions of points in the shape space (O'Higgins, 2000). Conversely non-isotropic landmark variation will result in non-isotropic variation in shape space. It is this variation that is interesting from a biological standpoint, as this non-isotropic variation is often the result of

climate, sex, age etc. Put simply, variation in shape of the object studied will be reflected in configurations of points in shape space.

It is this construction that underpins geometric morphometric theory, as each point in Kendall's shape space (curved) is represented by a configuration of points in Euclidean (linear) space, irrespective of scale, location or rotation (Adams et al., 2004).

2.2.4 Size

It is important to note that although GPA scales landmark formations, a measure of size is retained in the form of 'centroid size', although this is separate from the product of the GPA. As size is often biologically meaningful, it can be reintroduced as a variable to analyses as the natural logarithm of centroid size (Mitteroecker and Gunz, 2009). Natural log transformation is used in order to scale centroid size relative to the mean configuration (Dryden and Mardia, 1998).

2.2.5 Procrustes distances

The Procrustes distance between individual specimens, or group means, is a measure of the fit between specimens or groups. This is approximately the square root of the sum of squared differences between the positions of the landmarks after GPA and is related to the distance between specimens or groups in Kendall's shape space (Slice et al., 1996). Procrustes distances were calculated in MorphoJ (Klingenberg, 2008) and used in Manuscript 4.

2.2.6 Visualisation Techniques

One of the advantages of GMM is that the morphological differences measured may be visualised, allowing easy dissemination of results to even non-specialist audiences. The visualisation of morphological change is based on the ‘deformation’ of form. This originated with the use of transformation grids (Thompson, 1917) – inferring the shape change between points by their relative movement, illustrating how the shape of one part of an organism may be described as a distortion of the same part of another (Mitteroecker and Gunz, 2009, O’Higgins, 2000, Zelditch et al., 2004). With regard to GMM, deformation can be expressed between landmarks of the original and reference shapes using homology functions (matching points in the vicinity of one form to that of the other).

One of the problems with deformation and landmark based GMM analysis is that data between the landmarks is lost. To combat this the *thin plate spline* (TPS) interpolation is used (Bookstein, 1989, 1991) which computes a mapping function between two point configurations while the space in-between is smoothly interpolated by minimising the bending energy of the deformation, and results in only localised bending of the deformed surface (Dryden and Mardia, 1998).

For the images in this thesis a surface scan was taken of an adult domestic pig from the Anthropology Department Durham University teaching collection using a Konica Minolta V1-910 non-contact 3D digitiser. This scan was then morphed to represent different groups of pigs as required using the EVAN toolbox (2010). Images generated were used for visualisations in all four manuscripts.

2.2.7 Landmarks

Landmarks form the basis of most geometric morphometric methods. A landmark is a single point on an object, described by Cartesian co-ordinates, that it is biologically, evolutionarily homologous or mathematically equivalent between all specimens and samples under analysis. Homology has several meanings; in evolutionary studies it may be matching parts between organisms – as the structures share an evolutionary background they are therefore homologous (O'Higgins, 2000). In developmental studies physical structures may be matched through ontogenetic time, even though these structures may have re-modelled or moved, they are homologous through the continuity of the information they contain (Van Valen, 1982). Mathematical equivalence is concerned with the actual anatomical loci themselves (Zelditch *et al* 2004) rather than the structures they are associated with. When taken as a whole, a collection of landmarks should provide comprehensive coverage of the morphology of an object so that its whole form may be analysed, as landmarks are not considered individually, but as a formation. The information between landmarks is only inferred, meaning that inferences regarding form must be made on a general level, not a local one (O'Higgins and Jones, 1998). However, assuming the landmarks are placed on a structure so as to adequately describe its form, when the whole formation of points is analysed change in the shape of the points infers change in shape in the spaces between the points. This is true when visually modelling deformation e.g. using a thin-plate spline (Bookstein, 1991).

To aid the choice of homologous landmarks, Bookstein (1991) devised a series of categories to define landmarks, so that the investigator may determine how reliable

they are. There are 3 categories, Types 1, 2 and 3. Type 1 landmarks are considered optimal, Type 2 less so, and Type 3 landmarks are to be avoided if possible.

Type 1 landmarks are those defined with respect to discrete juxtapositions of tissues, such as triple points of suture intersections, they may be precisely identified and any forces that alter or move them may also be described. Type 2 landmarks lack such information in at least one direction, so forces that affect their position or form cannot easily be determined. Type 2 landmarks include extremities such as the tips of teeth or wings or the ends of bony processes. Type 3 landmarks are defined in juxtaposition to structures, like the endpoints of maximum length, breadth, etc., defined with respect to some distant structure. Landmarks that are derived from traditional metric measurements often fall into this category, being end points of measurements rather than morphologically derived points. Of these, the two- or three-dimensional locations of Types 1 and 2 are most often fully defined with respect to local morphology, and all dimensions are more-or-less biologically informative. Type 3 landmarks, however, are “deficient” in that they contain meaningful information only relative to the remote defining structure and are not defined in all directions (Bookstein, 1991, Slice, 2005, Zelditch et al., 2004).

Further to this classification, Zelditch *et al* (2004) derived five criteria to provide a guide to choosing landmarks for a shape study. They should be (1) homologous anatomical loci that (2) remain in their topological positions relative to other landmarks, (3) provide adequate coverage of the morphology, (4) can be found repeatedly and reliably, and (5) lie within the same plane.

From these descriptions it is obvious that as many type 1 landmarks should be included as possible and that type 3 landmarks should be avoided. However, in order to fulfil Zelditch *et al*'s (2004) third criterion (adequate coverage) this is often not possible, and type 3 landmarks must be used.

2.2.8 Data Collection

Each specimen is represented by a configuration of 44 three-dimensional cranial landmarks. Only unilateral data (the right side of the skull) were recorded. This decision was made to maximise data given the time constraints on data collection, and to reduce redundant variability. The data were collected using a 3-D Microscribe G2 digitiser (Immersion Corporation) by a single person (J.Owen) in order to eliminate inter-observer error. The skull was placed on its side, and supported so that there could be no movement when digitising was taking place.

2.2.9 Landmarks used and explanation for choice

The choice of landmarks was mainly based on the anatomy of the pig skull and the developmental biology behind its formation (Sack, 1982, Sisson and Grossman, 1910). It has also drawn upon classic zooarchaeological biometric practice (von den Driesch, 1976). The 44 landmarks used in this investigation are listed below with the land mark type (1, 2 or 3) given in brackets. The position of the landmarks is visualised in figures 10a and b.

- 1 Most anterior midline point on nasals (2).
- 2 Anterior join in nasal and pre maxilliar suture (2).
- 3 Anterior point of nasal (2).

- 4 Suture at the meeting point of the premaxillar, maxillar and nasal (1).
- 5 Most posterior point of superorbital foramen and groove (2).
- 6 Most lateral point of the Nuchal Crest (3).
- 7 Most anterior point of Nuchal Crest - on the midline of the parietal (3).
- 8 Most superior point of zygomatic process of temporal (2).
- 9 Most posterior point of zygomatic process of malar (2).
- 10 Superior point of the temporal process of malar (2).
- 11 Most inferior point of the malar (zygomatic arch) (3).
- 12 Anterior most point of the process emerging of the malar (zygomatic arch) (2).
- 13 Most posterior point of infraorbital foramen (2).
- 14 Most anterior point of infraorbital foramen (2).
- 15 Most superior point of the lower lacrimal foramina (2).
- 16 Most superior point of the occipital (3).
- 17 Most inferior point of the occipital (3).
- 18 Base of supraorbital process (2).
- 19 Anterior point of incisive foramen/palatine fissure (2).
- 20 Most posterior point of incisive foramen/palatine fissure (2).
- 21 Most anterior point of canine alveolus (2).
- 22 Most posterior point of canine alveolus (2).
- 23 Anterior point of the alveolar margin of the tooth row (2).
- 24-27 Contact points between M3/M2, projected labially (buccally) onto alveolar margin (2).
- 28 Most posterior point of the alveolar margin of the tooth row (2).
- 29-32 Contact points between M3/M2, projected lingually onto alveolar margin (2).

- 33 Most anterior point of the pterygoid process of the palatine (2).
- 34 Most lateral point of the pterygoid process of the palatine (2).
- 35 Most posterior point of the pterygoid process of the palatine (2).
- 36 Suture of the nasal and palatine bones (on the midline) (1).
- 37 Tip of posterior nasal spine (2).
- 38 Meeting point between the basisphenoid and basioccipital along midline, posterior of the vomer (1).
- 39 Anterior most point of the bulla tympanica (3).
- 40 Most anterior point of the paramastoid process (2).
- 41 Most anterior point on the margin of the Hypoglossal canal (2).
- 42 Lowest point on the orobasal border of foramen magnum (2).
- 43 Most posterior tip of occipital condyle (2).
- 44 Most superior point on the border of foramen magnum (2).

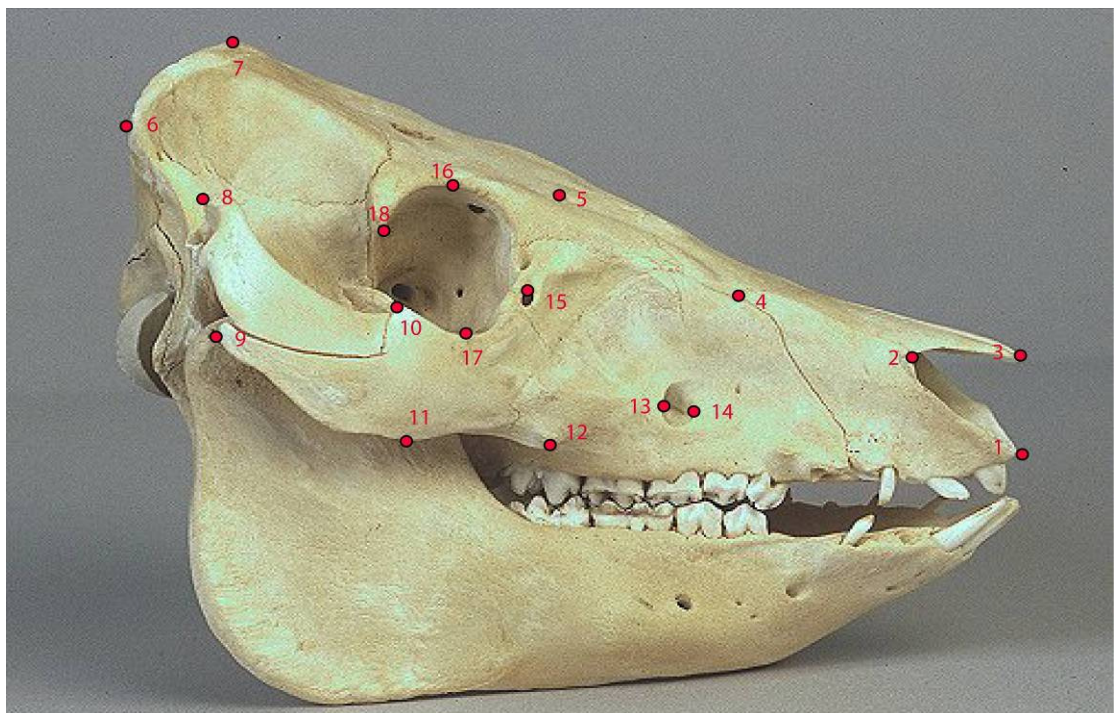


Figure 10a: Position of landmarks on the crania

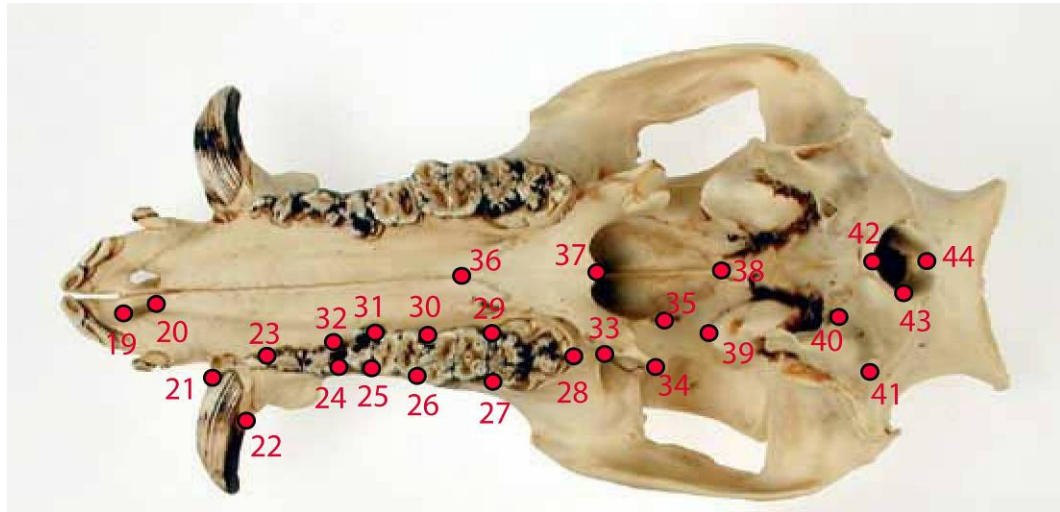


Figure 10b: position of landmarks on the basicranium

Of these 44 landmarks two are Type 1, thirty-six are Type 2 and six are Type 3. The majority of the landmarks are type 1 and 2 and suggest that the methodology should be adequate and not suffer from inherent bias. The 6 Type 3 landmarks (the top and bottom of the occipital and parietal and the tympanic bulla) have been chosen to represent areas of interest in anatomical regions where there are no Type 1 or 2 landmarks. Several obvious suture joints (such as between the frontal, nasal and maxilla) have not been included as these joints are not reliably observed on older animals, even though they appear on many younger individuals, due to continued bony growth and obliteration of the sutures.

In young individuals and Warthogs (*Phacochoerus africanus*) with their different dental formula, landmarks along the tooth row (24-27 and 29-32) are dropped, resulting in a configuration of 38 landmarks. This is noted where relevant in the papers of the results chapter.

2.2.10 Estimating intra-observer error

Method reliability and intra-observer error was assessed following the method proposed by O'Higgins and Jones (O'Higgins and Jones, 1998). A single cranium was digitised 10 times on separate days and compared with an unrelated reference collection (kindly provided by Dr Alastair McDonald from the Division of Veterinary Biomedical Sciences in Edinburgh University Royal (Dick) School of Veterinary Studies). GPA (see 2.2.2) and PCA (see 2.3.1) were then carried out on the data. The results are shown in Figure 13 (below), it shows the results of the PCA, depicting the first two PCs. All the repeats of the cranium used for reliability clusters at the negative end of PC1 (52% total variance) and the positive end of PC2 (16% total variance). The repeats are clustered tightly together, with several of the repeats plotting directly on top of each other. This indicates that errors of precision are small compared to sample variability, and that the landmarks chosen do not induce great amounts of random variation.

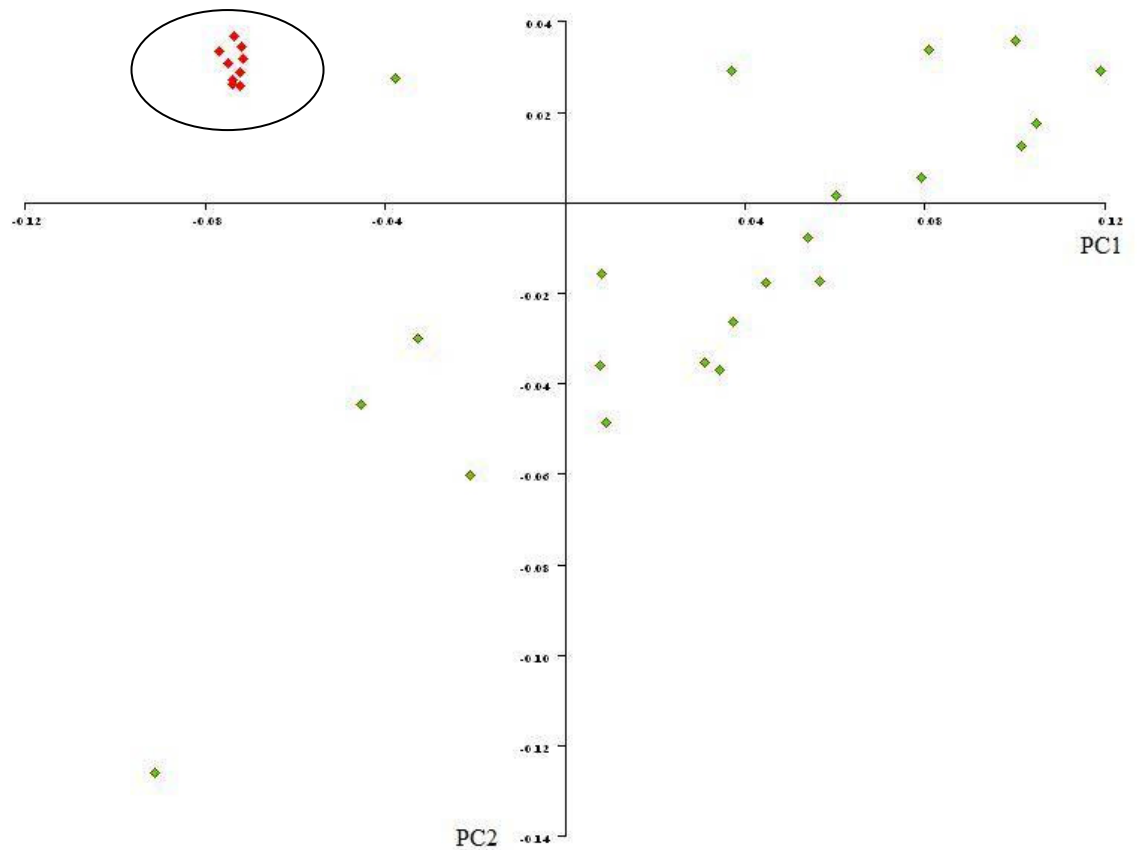


Figure 11: PCA showing 10 repeats of a single specimen in red, compared against a reference collection in green. Note the tight cluster of repeats in the top left hand corner (circled).

2.2.11 Sexual Dimorphism

Sus scrofa are notoriously difficult to sex on the basis of skeletal morphology (von den Driesch, 1976, Payne and Bull, 1988). The major difference between males and females is the form of the canine, which is larger and more curved in males, and in females has a channel running along the anterior side of the tooth (von den Driesch, 1976).

Size is frequently used for discrimination between the sexes. Males are held to be larger than females, but this is difficult to quantify in mixed wild-domestic

populations, as differences in size are also very notable between those groups. In early assemblages the wild pigs are larger, while in modern assemblages, where domestic pigs have received 'improved' or intensive breeding programs, domestic pigs are larger. These size differences are often greater than those due to sexual dimorphism and can easily override any sex related signal (Vigne et al., 2005).

No shape related sexual dimorphism has been catalogued in pigs using traditional biometric techniques. To test if there are any morphological differences solely attributable to sex that might influence the results of these investigations several tests were applied (Gonzalez et al., 2009). ANOVA was used to test size differences between the sexes, and MANOVA to test shape differences between the sexes. Two samples were used to test for sexual dimorphism, one of wild pigs from a single geographic region (Poland) to remove possible effects of climate or geographic variability, and a sample of domestic pigs (Deutsches Edelschwein - from East Germany) were also tested for sexual dimorphism.

Sexual dimorphism was found to be non-significant in wild pigs, both for centroid size ($p=0.71$, $df=1$, $F=0.14$), or shape ($p=0.27$, $df=125$, $F=1.07$), but was significant in domestic pigs (size $p=0.004$, $df=1$, $F=9.11$, shape $p<0.001$, $df=125$, $F=2.5$). For a pooled sample of wild and domestic pigs there was no sexual dimorphism in size ($p=0.37$, $df=1$, $F=0.83$), but there was in shape ($p<0.001$, $df=125$, $F=5.07$). Due to the small sample sizes available we conflated the males and females into a single sample - being aware that sexual dimorphism in the wild sample could potentially be a source of bias. However, mixing the male and females groups replicates conditions

found when analysing archaeological material, as it is difficult to assess the sex of pigs, especially in the absence of canines (von den Driesch 1976, Payne and Bull 1988).

2.2.12 Allometry

Allometry describes the relationship between body size and shape. In GMM it is the linear or linearised characterisation of the dependence of shape on size. This relationship is often the focus of studies, especially when describing shape change during ontogeny e.g. in primates (Mitteroecker et al., 2005), hippos (Weston, 2003) and marmots (Cardini and O'Higgins, 2005).

Allometry between adult specimens may be investigated using multivariate regression with log centroid size as the independent variable and PC scores as the multidimensional variables of shape. The correlation of shape, size and age is assessed and the significance of the angle of ontogenetic trajectories of pairs of populations tested using re-sampling and permutation tests (Viðarsdóttir et al., 2002, Mitteroecker et al., 2005). To remove the effects of allometry from a study, log size is regressed against shape and further analysis is then conducted on the regression residuals.

2.3 Methods of analysis

Detailed in this section are some of the common statistical methods used to analyse data in this thesis.

2.3.1 Principal Components Analysis (PCA)

Principal components analysis is widely used in morphometrics to simplify the exploration of shape variability by reducing the dimensionality of the data. It ranks co-variance factors (in the form of new variables or principal components) and gives each a score (as an eigenvalue) to describe what proportion of variance is described by each principal component.

The first step of PCA is to determine the direction of greatest variance; a vector which minimises the sum of squared distances between itself and the data points. This is the first principal component. Each subsequent principal component is computed the same way as the first, except that all correlation with preceding principal components has been removed, thus making each principal component independent. In effect, the first principal component describes the largest proportion of variance in the dataset, the second component describes the second largest proportion of variance and so on. This allows the majority of variance to be explained by a small number of principal components (typically the first few PCs summarise the majority of variance within the data), simplifying interpretations without the loss of much information (Rao, 1964).

Principal components can also be used as variables in their own right, replacing Procrustes fitted landmark scores. This is especially useful in datasets with high

degrees of dimensionality, as it can simplify analysis. By using only the scores on the first few principal components which typically contain most of the variation within the dataset, rather than all principal components, a summary of multidimensional data is created (Klingenberg and McIntyre, 1998). A degree of caution should be exercised when selecting PCs, so as not to remove potentially biologically meaningful variability and affecting the outcomes of further statistical tests.

Principal components scores can be used to identify clusters of data. It is useful to note that because PCA in this case is being computed from shape variables; visual references of variation can be generated by multiplying the original shape variables by the PC coefficients and summing them (Legendre and Legendre, 1998, Zelditch et al., 2004). PCAs were created in Morphologika2 (O'Higgins and Jones, 2006), MorphoJ (Klingenberg, 2008), the EVAN Toolbox (EVAN Toolbox, 2010) or SPSS (© Microsoft Corporation) and used in all four Manuscripts.

2.3.2 Canonical Variates Analysis (CVA)

Canonical variates analysis (CVA) is a method used to find the shape features that best distinguish multiple groups of specimens that have been defined prior to analysis (Slice et al., 1996). It is frequently used in an exploratory style to visually assess the separation of groups, and the presence of areas of high or low data density (Mitteroecker and Bookstein, 2011). It is designed to simplify descriptions of differences between groups that are mutually exclusive (i.e. they vary by a categorical variable), which can include traits such as sex and species, these are sometimes known as 'qualitative traits' or 'grouping variables'. Generally these traits should be discontinuous but sometimes continuous variation can be graded and

classified like discontinuous variation (for example where information is limited or occurs along a graded scale). Where this occurs such continuous traits are treated as separate groupings for the purpose of the analysis, but limits the inferences that may be drawn from the conclusions (Zelditch et al., 2004).

CVA finds linear transformations of the data which maximize the among group variation relative to the pooled within-group variation. The canonical variates may then be displayed as an ordination to show the group centroids and scatter within groups. This gives a new co-ordinate system by which the position of each group may be described. This may be thought of as a 'data reduction' method in the sense that one wants to describe among group differences in few dimensions. The vectors of coefficients are orthogonal as in Principal Component Analysis, although the canonical variates are uncorrelated with each other (Dryden and Mardia, 1998; Slice et al., 1996). CVs are not a complete description of the differences between groups, they represent the part of the difference between groups that is most useful discriminating between them, the part that has the least variation within groups relative to the difference between them (Zelditch et al., 2004).

CVA produces results that look quite different to those produced by PCA for two reasons. Firstly, CVA maximises differences between groups, and this is often different to how individuals differ. Secondly, CVA re-scales to axes that optimise between group variation relative to within group variation. This difference between PCA and CVA can be useful to illustrate which shape vectors are causing shape change. CVA can represent dissimilarity between groups of specimens in a two dimensional scatter plot as it has maximised the differences between them on a single

CV (Mitteroecker and Bookstein, 2011), where as PCA may spread the differences between groups on multiple vectors (PCs), making it hard to illustrate the difference between groups in two dimensional plots, although the differences on individual PCs may point to potential sources of biologically meaningful variation between samples that would be harder to spot on a CVA. CVAs were created in MorphoJ (Klingenberg, 2008) and used in Manuscripts 1 and 2.

2.3.3 Permutation Tests

Permutation tests resample groups without replacing them, in this thesis they are used to assess the reliability of CVAs (2.3.2) and regression analysis (2.3.8). Groups are randomly re-assigned, or permuted, a set number of times and pair-wise differences in the means of the permuted sets are calculated. The proportion of times in which the difference between the means of the permuted sets exceed that of the original groups is taken as the probability that the observed value could have arisen by a random splitting of the underlying distribution (Zelditch et al., 2004). Permutation tests were computed in MorphoJ (Klingenberg, 2008) and SAS, in manuscripts 1, 2 and 4.

2.3.4 Discriminant Functions (DFA)

Discriminant function analysis (DFA) examines the separation between two or more groups known prior to analysis, testing the hypothesis that members of these groups are distinguishable. DFA determines whether group means differ and then predicts group affiliation on the basis of discriminant functions (Sneath and Sokal, 1973). These are derived by building linear combinations of the original variables that maximize between to within-group variance. The groups are clustered around the

mean discriminant score (the centroid) for each group, for each function. Classification is based on each case's proximity to the groups' centroid, and probabilities are calculated to express the likelihood that the case belongs to each of the groups. The smallest distance and highest probability determines the case's group assignment (Kovarovic et al., 2011).

This can be conducted between multiple groups so that they are analysed within the same shape space, which will produce distances (Mahalanobis' or Procrustes distances) between pairs of groups (Zelditch et al., 2004). As the multivariate space is scaled by the inverse of the pooled within group variation, distances within this transformed space are independent of the scale of measurement and differences are expressed in units of standard deviations. The result is that even though discriminant axes can be visualized as shape deformations, they should not be interpreted as meaningful biological factors due to this rescaling (Bookstein, 1991, Mitteroecker and Bookstein, 2011). Therefore, DFA is most useful for comparisons of specific groups, whereas CVA may be more useful for general analysis of group structure in a dataset (Klingenberg and Monteiro, 2005). The reliability of DFA in discriminating between groups is tested with leave-one-out-cross-validation (see below) (Zelditch et al., 2004). DFA was used in manuscripts 1 and 3, they were conducted in MorphoJ (Klingenberg, 2008) and R (R Development Core Team, 2008).

2.3.5 Cross Validation

Discriminant functions and CVA frequently over fit data. DFA must provide group assignment for each individual and it maximises differences between groups which can result in a higher rate of correct assignment than chance alone would allow, even

in datasets that have fictional relationships (Kovarovic et al., 2011). To avoid the effects of such over fitting re-sampling techniques are employed. Two types were used in this thesis, leave-one-out cross-validation with discriminant functions, and permutation tests (see 2.3.3) with CVA and regressions.

Cross validation assesses how accurately a predictive model will perform in practice. Data are partitioned into complementary datasets, performing analysis on one subset (called the *training set*), and validating the analysis on the other subset (called the *validation set*). Multiple rounds are performed using different subsets and the results averaged. Leave-one-out-cross-validation partitions a single observation as the validation set, and uses the remaining dataset as the training set. This is repeated so that each observation is used once as the validation set, producing k numbers of cross-validations, where k is the number of observations in the dataset (Lauchenbruch, 1967). Cross validations were conducted in MorphoJ (Klingenberg, 2008) and R (R Development Core Team, 2008).

2.3.6 Student's and Hotelling's t -tests

t -Tests are used to compute the significance of differences between group means. A t -test evaluates the probability that two samples with means differing by an observed amount could be explained by random sampling from a single population within the overall variance.

Student's t -test compares the means of two groups of univariate data (e.g. size) in order to test the hypothesis of equality between the means. It determines whether any difference is due to random variation or is statistically significant (Legendre and

Legendre, 1998). Hotelling's t -test is a generalisation of students t statistic (Hotelling, 1931) used with multivariate data. It compares multiple means at the same time by computing the mean vector between two groups, testing the hypothesis that two groups originate from populations with the same centroid (e.g. shape) (Legendre and Legendre, 1998). t -Tests were conducted in Excel and SPSS (© Microsoft Corporation).

2.3.7 ANOVA and MANOVA

Significance between groups can be assessed without computing group means using ANOVA. ANOVA stands for *analysis of variance*, where by the variance explained by a categorical variable is compared the variance it does not explain. This ratio (explained variance divided by the unexplained variance) is given as the F statistic. The F -value is the probability of an equal or larger F -ratio for two samples drawn randomly from the same distribution (Legendre and Legendre, 1998).

ANOVA compares variation within groups to variation between groups. As such it can be used to examine differences between multiple groups, and multiple categorical variables. In this thesis ANOVA is used mainly to examine differences in size between groups.

Differences in shape are assessed using either Hotelling's T^2 test (to test for differences between two group means (see 2.3.6) or MANOVA where there are more than two groups. MANOVA stands for *multivariate analysis of variance* and like ANOVA it compares means between groups, but does it for means in multivariate data, like shape. Shape is a single, complex trait described by several continuous

components, to analyse it a multivariate version of the F -statistic is needed, one that is also a function of the within-group and between-group variance. A common statistic to fulfil this is Wilks-Lambda, which is a product of the non-zero eigenvalues of the variance-covariance matrices of the groups in question (Legendre and Legendre, 1998, Zelditch et al., 2004). These were computed in MorphoJ (Klingenberg, 2008), and in Excel and SPSS (© Microsoft Corporation), they were used in all four Manuscripts.

2.3.8 Regression

Regression is used to estimate and describe the relationship between a dependent (generally a random) variable (y) and a set of independent (explanatory) variables (x), to predict the values of y for given values of x (Legendre and Legendre, 1998). In geometric morphometrics it is often used to test the relationship between size and shape (Meloro et al., 2008, Mitteroecker et al., 2005), or size or shape against other continuously valued factors such as latitude, longitude or climate (Cardini et al., 2007).

In a simple linear regression there is a single x and y variable. The regression here attempts to draw an optimised straight line (hence the name linear) through a scatter of points for which x and y are known. Resolution of the regression allows an estimation of y for any value of x (Legendre and Legendre, 1998).

To investigate shape, which is a multidimensional variable, multivariate regression is required. This is the regression of several dependent variables (e.g. multidimensional shape) onto a single independent variable (e.g. size or temperature). The coefficients

obtained by multivariate regression are the same as those estimated by bivariate regression but the tests of significance used are Wilks' Lambda, or in the case of regression of shape and size Goodall's *F*-statistic (Zelditch et al., 2004). Rather than run regression on Procrustes fitted co-ordinates, principal components scores are used as they have the correct degrees of freedom ($3k-7$ – where k is the number of landmarks – see section 2.2.2). This also allows a reduced data set to be run, in cases where there is high dimensionality that may not be biologically meaningful (Zelditch et al., 2004).

Multiple linear regressions can be either multivariate or bivariate, and are used with one (bivariate) or more (multivariate) dependent variables and two or more independent variables. The relationship between the dependent variables (y) and the independent variables (x) is still scalar, in the same manner as a simple multiple regression (Legendre and Legendre, 1998). Multiple multivariate regressions can be used to explore wider relationships of shape and size, e.g. with climate - including permutations of temperature and precipitation (Cardini and Elton, 2009).

Regressions were computed in Excel and SPSS (© Microsoft Corporation), MorphoJ (Klingenberg, 2008) and Morphologika2 (O'Higgins and Jones, 2006). Linear and multiple multivariate regressions were used in Manuscript 2 and in Manuscript 4.

2.3.9 Cluster Analysis and Neighbour Joining Trees

Cluster analysis is a hierarchical method of summarising a multivariate distance matrix between specimens in a single diagram (Slice et al., 1996). The diagram can either be a tree like, called a dendrogram, or a network. Cluster analysis assigns a set

of objects into groups (called clusters) so that the objects in the same cluster are more similar to each other than to those in other clusters. There are many different types of algorithms used, but in GMM a widely used method is neighbour joining (NJ) (Saitou and Nei, 1987) which builds phonetic trees (phenograms) or networks.

Neighbour joining takes as input a distance matrix specifying the distance between each pair of individuals, taxa or groups. In this thesis Procrustes distances were used. NJ determines which pair has the lowest value (smallest distance) and joins these neighbouring groups to the tree or network with a node, which is then fixed in place. The distance matrix is then recalculated, replacing the pair of joined neighbours with the node, determining the distance from each of the groups to the node. This process is iterative, until till all the groups are joined. NJ is a simple model as makes no assumptions of the data (Legendre and Legendre, 1998). NJ trees were computed in NTsys 2.1 (Rohlf, 2008) and used in Manuscripts 1 and 2.

2.3.10 Mode of evolution

In manuscript 1 the mode of evolution of Suids was investigated to elucidate the evolutionary history of the African genus *Potamochoerus*. This was first assessed by studying the scaling relationship of shape divergence and time since common ancestry. Here morphological (Procrustes) distances are used for shape divergence and genetic distances stand proxy for evolutionary time (Gomez-Robles and Polly, 2012). This reveals whether the mode of evolution in the family Suidae results from long-term directional, stabilizing, or randomly varying selection (Polly, 2004, 2008, Gomez-Robles and Polly, 2012).

Distances between pairs of species were plotted on a scatter graph with genetic distances on the x axis and Procrustes on the y. The mode of evolution was determined by assessing whether the scaling of morphological divergence is linear with respect to the genetic distances (directional or diversifying divergence); curvilinear as the square-root of genetic distance (Brownian motion); or flat (stabilizing selection or stasis), using Maximum Likelihood (Gomez-Robles and Polly, 2012) to estimate the evolutionary mode coefficient from the following equation:

$$P = t^a$$

where P is morphological divergence, t is time since common ancestry (genetic distance serves as the proxy for this), and a is the mode coefficient ranging from 0.0 to 1.0. In a random walk process phenotypes diverge with the square root of time (0.5); in a directional process divergence is linear with time (1.0); and in perfect stasis there is no divergence with time (0.0) (Polly, 2008, Polly, 2004, Gomez-Robles and Polly, 2012). The number of independently evolving variables refers to the number of significant principal components contributing towards the Procrustes distance score.

To determine the mode of evolution responsible for the previously observed incongruence between *Potamochoerus* and *Sus*, the phylogenetic tree was projected into suid morphospace (Polly, 2004, 2008, Gomez-Robles and Polly, 2012, Rohlf, 2002). Cranial shape scores for species were reconstructed at the ancestral nodes of the phylogenetic tree (Gongora et al., 2011) following the methodology of Martins and Hanson (see equations 4 and 5) (Martins and Hansen, 1997), and projected into morphospace with a linear extrapolation along the branches (Polly, 2008). The

projections were constructed by plotting PC scores for each node and genus. The nodes were connected in order of last common ancestor and the genera to the nearest ancestral node. This generalised linear model method assumes a Brownian Motion mode of evolution and is inherently conservative. This model was used to reveal the relationship between morphology and genetic ancestry in suids. Mode of evolution analysis was conducted in Mathematica 8.

Bibliography

- ADAMS, D. C., ROHLF, F. J. & SLICE, D. E. 2004. Geometric morphometrics: Ten years of progress after the "revolution". *Italian Journal of Zoology*, 71, 5-16.
- ALBARELLA, U. 2002. *Size matters: how and why biometry is still important in zooarchaeology*, Oxford, Oxbow Books.
- BOOKSTEIN, F. L. 1989. Principle warps: thin-plate splines and the decomposition of deformations. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 11, 567-585.
- BOOKSTEIN, F. L. 1991. *Morphometric tools for landmark data: geometry and biology*, New York, Cambridge University Press.
- BOOKSTEIN, F. L. 1996a. Combining the tools of geometric morphometrics. In: MARCUS, L. F., CORTI, M., LOY, A., NAYLOR, G. & SLICE, D. E. (eds.) *Advances in morphometrics*. New York: Plenum.
- BOOKSTEIN, F. L. 1996b. Standard formula for the uniform shape component in landmark data. In: MARCUS, L. F., CORTI, M., LOY, A., NAYLOR, G. & SLICE, D. E. (eds.) *Advances in Morphometrics*. New York: Plenum.
- CARDINI, A. & ELTON, S. 2009. Geographical and taxonomic influences on cranial variation in red colobus monkeys (Primates, Colobinae): introducing a new approach to 'morph' monkeys. *Global Ecology and Biogeography*, 18, 248-263.
- CARDINI, A., JANSSON, A. U. & ELTON, S. 2007. A geometric morphometric approach to the study of ecogeographical and clinal variation in vervet monkeys. *Journal of Biogeography*, 34, 1663-1678.
- CARDINI, A. & O'HIGGINS, P. 2005. Post-natal ontogeny of the mandible and ventral cranium in *Marmota* (Rodentia, Sciuridae): allometry and phylogeny. *Zoomorphology*, 124, 189-203.
- DOBNEY, K. & ERVYNCK, A. 2000. Interpreting developmental stress in archaeological pigs: The chronology of linear enamel hypoplasia. *Journal of Archaeological Science*, 27, 597-607.
- DRYDEN, I. L. & MARDIA, K. V. 1998. *Statistical Shape Analysis*, New York, John Wiley and Sons.
- EVAN TOOLBOX. 2010. <http://evan-society.org/node/42> [Online].
- GOMEZ-ROBLES, A. & POLLY, P. D. 2012. Morphological Integration in the Hominin dentition: Evolutionary, Developmental, and Functional Factors. *Evolution*, 66, 1024-1043.
- GONGORA, J., CUDDAHEE, R. E., NASCIMENTO, F. F. D., PALGRAVE, C. J., LOWDEN, S., HO, S. Y. W., SIMOND, D., DAMAYANTI, C. S., WHITE, D. J., TAY, W. T., RANDI, E., KLINGEL, H., RODRIGUES-ZARATE, C. J., ALLEN, K., MORAN, C. & LARSON, G. 2011. Rethinking the evolution of extant sub-Saharan African suids (Suidae, Artiodactyla). *Zoologica Scripta*, 40, 327-335.
- GONZALEZ, P. N., BERNAL, V. & PEREZ, I. 2009. Geometric morphometric approach to sex estimation of human pelvis. *Forensic Science International*, 189, 68-74.
- GOWER, J. C. 1975. Generalized Procrustes analysis. *Psychometrika*, 40, 33-51.
- GREENFIELD, H. J. & ARNOLD, E. R. 2008. Absolute age and tooth eruption and wear sequences in sheep and goat: determining age-at-death in zooarchaeology using a modern control sample. *Journal of Archaeological Science*, 35, 836-849.

- GROVES, C. 1981. *Ancestors for the Pigs: Taxonomy and Phylogeny of the Genus Sus*, Canberra, Research School of Pacific Studies, Australian National University.
- HIGHAM, C. F. W. 1967. Stock Rearing as a Cultural Factor in Prehistoric Europe. *Proceedings of the Prehistoric Society*, 33, 84-106.
- HOTELLING, H. 1931. The generalization of Student's ratio. *Annals of Mathematical Statistics* 2, 360-378.
- JONES, G. G. 2006. Tooth eruption and wear observed in live sheep from Butser Hill, the Cotswold Farm Park and five farms in the Pentland Hills, UK. In: Ruscillo, D. (ed.) *Recent Advances in Ageing and Sexing Animal Bones*. Oxford: Oxbow Books. 155-178.
- KENDALL, D. 1977. The Diffusion of Shape. *Advances in Probability*, 9, 428-430.
- KENDALL, D. 1984. Shape manifolds, Procrustean metrics and complex projective spaces. *Bulletin of the London Mathematical Society*, 16, 81-121.
- KLINGENBERG, C. P. 2008. *MorphoJ* [Online]. University of Manchester, UK.: Faculty of Life Sciences. Available: http://www.flywings.org.uk/MorphoJ_page.htm.
- KLINGENBERG, C. P. & MCINTYRE, G., S 1998. Geometric morphometrics of developmental instability: Analyzing patterns of fluctuating asymmetry with procrustes methods. *Evolution*, 52, 1363-1375.
- KLINGENBERG, C. P. & MONTEIRO, L. R. 2005. Distances and directions in multidimensional shape spaces: implications for morphometric applications. *Systematic Biology*, 54, 678-688.
- KOVAROVIC, K., AIELLO, L. C., CARDINI, A. & LOCKWOOD, C. A. 2011. Discriminant function analyses in archaeology: are classification rates too good to be true? *Journal of Archaeological Science*, 38, 3006-3018.
- LAUCHENBRUCH, P. A. 1967. An almost unbiased method of obtaining confidence intervals for the probability of misclassification in discriminant analysis. *Biometrics*, 23, 639-645.
- LEGATES, D. R. & WILLMOTT, C. J. 1990a. Mean seasonal and spatial variability in gauge-corrected global precipitation. *International Journal of Climatology*, 10, 111-127.
- LEGATES, D. R. & WILLMOTT, C. J. 1990b. Mean seasonal and spatial variability in global surface air temperature. *Theoretically Applied Climatology*, 41, 11-21.
- LEGENDRE, P. & LEGENDRE, L. 1998. *Numerical Ecology: Second English Edition*, Oxford, Elsevier.
- MARTINS, E. P. & HANSEN, T. F. 1997. Phylogenies and the Comparative Method: A General Approach to Incorporating Phylogenetic Information into the Analysis of Interspecific Data. *The American Naturalist*, 149, 646-667.
- MEADOW, R. 1981. Early Animal Domestication in South Asia: a First Report of the Faunal Remains from Mehrgarh, Pakistan. In: HARTEL, H. (ed.) *South Asian Archaeology 1979*. Berlin: Dietrich Reimer Verlag.
- MEADOW, R. 1999. The use of size index scaling techniques. In: BECKER, C., MANHART, H., PETERS, J. & SCHIBLER, J. (eds.) *Festschrift Fur Angela von den Driesch*. Rahden/Westf.: Verlag Marie Leidorf GmbH.
- MELORO, C., RAIA, P., PIRAS, P., BARBERA, C. & O'HIGGINS, P. 2008. The shape of the mandibular corpus in large fissiped carnivores: allometry, function and phylogeny. *Zoological Journal of the Linnean Society*, 154, 832-845.

- MITTEROECKER, P. & BOOKSTEIN, F. L. 2011. Linear Discrimination, Ordination, and the Visualization of Selection Gradients in Modern Morphometrics. *Evolutionary Biology*, 38, 100–114.
- MITTEROECKER, P. & GUNZ, P. 2009. Advances in Geometric Morphometrics. *Evolutionary Biology*, 36, 235–247.
- MITTEROECKER, P., GUNZ, P. & BOOKSTEIN, F. L. 2005. Heterochrony and geometric morphometrics: a comparison of cranial growth in *Pan paniscus* versus *Pan troglodytes*. *Evolution & Development*, 7, 244–258.
- O'HIGGINS, P. 2000. The study of morphological variation in the hominid fossil record: biology, landmarks and geometry. *Journal of Anatomy*, 197, 103–120.
- O'HIGGINS, P. & JONES, N. 1998. Facial growth in *Cercocebus torquatus*: an application of three-dimensional geometric morphometric techniques to the study of morphological variation. *Journal of Anatomy*, 193, 251–272.
- O'HIGGINS, P. & JONES, N. 2006. *Tools for statistical shape analysis* [Online]. Hull York Medical School. Available: <http://sites.google.com/site/hymsfme/resources>.
- PAYNE, S. 1973. Kill-off patterns in sheep and goats: the mandibles from Asvan Kale. *Anatolian Studies*, 23, 281–303.
- PAYNE, S. & BULL, G. 1988. Components of variation in measurements of pig bones and teeth, and the use of measurements to distinguish wild from domestic pig remains. *Archæozoologia*, 2, 27–65.
- POLLY, P. D. 2004. On the simulation of the evolution of morphological shape: multivariate shape under selection and drift. *Palaeontologia Electronica*, 7.2.7A, 28.
- POLLY, P. D. 2008. Adaptive Zones and the Pinniped Ankle: A 3D Quantitative Analysis of Carnivoran Tarsal Evolution. In: SARGIS, E. & DAGOSTO, M. (eds.) *Mammalian Evolutionary Morphology: A Tribute to Frederick S. Szalay*. Dordrecht, The Netherlands: Springer.
- R DEVELOPMENT CORE TEAM 2008. *R: A language and environment for statistical computing*, Vienna, Austria, R Foundation for Statistical Computing.
- RAO, C. R. 1964. The Use and Interpretation of Principal Component Analysis in Applied Research. *Sankhyā: The Indian Journal of Statistics, Series A (1961-2002)*, 26, 329–358.
- REITZ, E. & WING, E. 1999. *Zooarchaeology*, Cambridge, Cambridge University Press.
- ROHLF, F. J. 1996. Morphometric spaces, shape components, and the effects of linear transformations. In: MARCUS, L. F., CORTI, M., LOY, A., NAYLOR, G. & SLICE, D. E. (eds.) *Proceedings of the 1993 NATO Advanced Studies Institute on Morphometrics in Il Ciocco, Italy*. New York: Plenum.
- ROHLF, F. J. 1997. *tpsSmall*, Stony Brook, NY., Department of Ecology and Evolution, State Univ. New York.
- ROHLF, F. J. 1998. On Applications of Geometric Morphometrics to Studies of Ontogeny and Phylogeny. *Systematic Biology*, 47, 147–158.
- ROHLF, F. J. 2002. Geometric morphometrics and phylogeny In: MACLEOD, N. & FOREY, P. L. (eds.) *Morphology, Shape and Phylogeny*. CRC Press.
- ROHLF, F. J. 2008. *NTSYSpc: Numerical Taxonomy System* [Online]. Setauket, NY: Exeter Publishing, Ltd.

- SACK, W. O. 1982. *Essentials of Pig Anatomy: Horowitz/Kramer Atlas of Musculoskeletal Anatomy of the Pig*, Ithaca, New York, Veterinary Textbooks.
- SAITOU, N. & NEI, M. 1987. The Neighbor-joining Method: A New Method for Reconstructing Phylogenetic Trees. *Molecular Biology and Evolution*, 4, 406-425.
- SCHNEIDER, A. 2012. *GPS Visualiser* [Online]. Available: <http://www.gpsvisualizer.com/>.
- SILVER, I. A. 1969. The ageing of domestic animals. In: BROTHWELL, D. & HIGGS, E. S. (eds.) *Science in Archaeology*. London: Thames and Hudson. 283-302.
- SISSON, S. & GROSSMAN, J. D. 1910. *The Anatomy of the Domestic Animals*, Philadelphia and London, W. B. Saunders and Company.
- SLICE, D. E. 2001. Landmark coordinates aligned by procrustes analysis do not lie in Kendall's shape space. *Systematic Biology*, 50, 141-149.
- SLICE, D. E. 2005. Modern Morphometrics. In: SLICE, D. E. (ed.) *Modern Morphometrics in Physical Anthropology*. New York: Kluwer Academic/Plenum Publishers.
- SLICE, D. E., BOOKSTEIN, F. L., MARCUS, L. F. & ROHLF, F. J. 1996. A glossary for geometric morphometrics. In: MARCUS, L. F., CORTI, M., LOY, A., NAYLOR, G. & SLICE, D. E. (eds.) *Advances in Morphometrics*. New York: Plenum.
- SNEATH, P. & SOKAL, R. 1973. *Numerical taxonomy: The principles and practice of numerical classification*, San Francisco, W. H. Freeman.
- THOMPSON, D. W. 1917. *On Growth and Form*, London, Cambridge University Press.
- VAN VALEN, L. 1982. Homology and causes. *Journal of Morphology*, 173, 305-312.
- VIÐARSDÓTTIR, U. S., O'HIGGINS, P. & STRINGER, C. 2002. A geometric morphometric study of regional differences in the ontogeny of the modern human facial skeleton. *Journal of Anatomy*, 201, 211-229.
- VIGNE, J.-D., HELMER, D. & PETERS, J. 2005. New archaeological approaches to trace the first steps of animal domestication: general presentation, reflections and proposals. In: VIGNE, J. D., PETERS, J. & HELMER, D. (eds.) *First Steps of Animal Domestication: New Archaeological Approaches*. Oxford: Oxbow Books.
- VON DEN DRIESCH, A. 1976. *A Guide to the Measurement of Animal Bones from Archaeological Sites*, Cambridge, MA, Peabody Museum Bulletin 1.
- WESTON, E. M. 2003. Evolution of ontogeny in the hippopotamus skull: using allometry to dissect developmental change. *Biological Journal of the Linnean Society*, 80, 625-638.
- WILLMOTT, C. J. & FEDDEMA, J. J. 1992. A more rational climatic moisture index. *Professional Geography*, 44, 84-88.
- WILLMOTT, C. J. & MATSUURA, K. 2001. *Terrestrial air temperature and precipitation: monthly and annual climatologies* [Online]. Newark: University of Delaware,. Available: http://climate.geog.udel.edu/climate/html_pages/archive.html.
- ZEDER, M. A. 2006. A Critical Assessment of Markers of Initial Domestication in Goats (*Capra hircus*). In: ZEDER, M.A., BRADLEY, D.G., EMSHWILLER, E., & SMITH, B.D., (eds.) *Documenting Domestication: New Genetic and*

Archaeological Paradigms. Berkeley, Los Angeles, London: University of California Press.

ZELDITCH, M. L., DONALD, L., SWIDERSKI, H., SHEETS, D. & FINK, W. L.
2004. *Geometric Morphometrics for Biologists: A Primer*, London, Elsevier Academic Press.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18

Chapter 3
Manuscript 1

Resolving genetic and morphological phylogenies within
Suidae

Title: Resolving genetic and morphological phylogenies within Suidae

Running head: Resolving genetic and morphological incongruence in pigs

Joseph Owen^{1,2}, P. David Polly³, Keith Dobney⁴, Allowen Evin^{4,5}, Helgi Gunnarsson⁶, Greger Larson⁷ and Una Strand Vidarsdottir^{2*}

¹*Department of Archaeology, Durham University, South Road, DH1 3LE, UK*

²*Department of Anthropology, Durham University, South Road, DH1 3LE, UK*

³*Departments of Geological Sciences, Biology, Anthropology, Indiana University Bloomington, 1001 E. 3rd St. Jordan Hall 142 Bloomington, IN, 47405-7005 USA*

⁴*Department of Archaeology, University of Aberdeen, St Mary's Building, Elphinstone Road, AB24 3UF, UK*

⁵*Centre National de la Recherche Scientifique, 3 Rue Michel-Ange, 75794 Paris, France*

⁶*EVAN Society, University of Vienna, Althanstraße 14, A-1090 Wien, Austria*

⁷*Durham Evolution and Ancient DNA, Department of Archaeology, Durham University, South Road, DH1 3LE, UK*

**Corresponding author: una.vidarsdottir@durham.ac.uk*

Abstract

Phenetic trees derived from morphology often differ from independently estimated phylogenetic trees, usually as a result of convergent or parallel evolution. Within the family Suidae, there is marked incongruence between the morphological and genetically derived relationships between the sub-Saharan African genus *Potamochoerus* and the Eurasian *Sus*. Genetic studies place sub-Saharan African pigs in a monophyletic clade but morphological analyses suggest that *Potamochoerus* is more closely related to *Sus* than to other sub-Saharan pigs. These conflicting interpretations hamper a resolution of the systematics of this group and confound efforts to understand whether suid colonisation of the African continent occurred once or multiple times. In order to understand the source of the conflicting topologies, we applied geometric morphometrics and multivariate statistics to 38 unilateral homologous landmarks from 471 African and Eurasian suids. We then

53 reconstructed the ancestral node of Suidae and tested the mode of evolution.
54 *Potamochoerus* is genetically more closely related to African genera but like *Sus*, it
55 possesses a generalist morphology and occupies the same ecological niche. This
56 shared generalist behaviour, a direct consequence of the evolutionary history of
57 *Potamochoerus*, is the principal reason why morphology alone fails to reveal the
58 monophyly of African suids.

59

60 **Introduction**

61 The family Suidae is one of the most geographically widespread of extant terrestrial
62 mammals. Suids inhabit six continents as a result of both natural dispersal and
63 human-mediated introductions [1]. Despite their abundance, our understanding of
64 their evolutionary history and dispersal [2, 3], the monophyletic status of some
65 genera, and the phylogenetic relationships within the genus *Sus* [4], remains
66 incomplete. More specifically, there is marked disparity between the position of sub-
67 Saharan *Potamochoerus* and Eurasian *Sus* on trees constructed using genetic and
68 morphological data. While genetic data [3] reveal a deep split between these genera,
69 morphological studies show striking similarities in cranial shape [3, 5, 6].
70 Explanations for this disparity include: retention of ancestral traits [3, 7], parallel
71 evolution in response to dietary pressures [3, 7], and convergence due to inhabiting
72 similar ecological niches [5].

73

74 Combining and contrasting information from morphology and genetics is rapidly
75 becoming an important area of taxonomic research [8]. Morphological studies have
76 quantified the integration and modularity of phylogenetic signals within structures
77 [9] and assessed the strength of phylogenetic signals in the phenotype by quantifying
78 the congruence between phylogenetic and phenetic trees [10]. Alternative approaches
79 project the phylogenetic signal within morphological space, in order to visualise the
80 phylogenetic history of phenotype [11, 12], while genetic studies have investigated
81 the effect of genes on morphological diversity [13] through multivariate quantitative
82 genetics [14].

83

84 Using morphometric data to estimate evolutionary relationships remains
85 controversial [9, 10], since the topologies of phylogenetic trees derived from
86 phenotypes rarely match those derived from genotypes [15]. This incongruence

87 results from phenotypic history including both adaptive and non-adaptive genetic
88 components in conjunction with non-genetic environmental factors. As a result,
89 morphometric data always possesses both phylogenetic and non-phylogenetic signals
90 [10]. Phenotypic change is also complicated because it involves both quantitative
91 changes in existing morphological structures, transformations which may not have a
92 linear relationship with the underlying genetic changes [8], and the addition of
93 ‘novel’ structures (i.e. structures that are not homologous to those found in the
94 ancestral morphology) [16]. Furthermore, phylogenetic signal is weakened by
95 parallel evolution and convergence [15]. Methods used to map shape variation onto
96 independent phylogenies have been well tested and can now account for the mode of
97 evolution and explain incongruence between morphology and genetics [8, 17].

98
99 An integrated application of genetic and morphological taxonomic approaches has
100 the potential to provide alternative and deeper insights into species’ developmental
101 history, especially when there are marked topological differences in the evolutionary
102 trees they generate. Perhaps the best-documented example can be found in the order
103 Cetartiodactyla, where both the sister taxon of Cetacea and the monophyly of
104 specific clades are uncertain. Genetic studies place Cetacea with Hippopotamidae
105 [18, 19], whereas studies of morphology place Cetacea with the extinct family
106 Raoellidae and Hippopotamidae with Suina [20, 21]. A reconciliation has been
107 suggested by studies combining topologies from trees generated by genetics and
108 morphology [22, 23], studies combining Hippopotamidae molecular and fossil data
109 [24, 25] and a re-evaluation of earlier morphological work in light of the genetic
110 discoveries [26, 27]. All of these approaches support the existence of a separate
111 Cetancodonta clade (Hippopotamidae + Cetacea).

112
113 Both genetics [3, 28, 29] and morphology [4-6, 30, 31] have been used to study suid
114 systematics, but have only been combined in one regional study of *Sus* species in
115 Island South East Asia (ISEA) [32]. Here, we present the results of a large-scale
116 study of the family Suidae undertaken to resolve the incongruence between
117 *Potamochoerus* and *Sus*. In doing so, we established the details of the incongruence
118 between the genetic and morphological trees of 10 suid taxa studied, and compared
119 phenotypic relationships with known phylogenetic relationships. We then modelled
120 the overall mode of evolution of suids and compared the individual genera with this

overall mode to determine whether their evolution was directed or constrained. Finally, we generated the ancestral shape scores of suids by projecting the genetic tree into morphospace to map the evolution of each genus. This provided an explanation for the apparent incongruence in the genetic and morphological relationships and revealed the evolutionary history of the African branch of the suid family.

Materials and Methods

We analysed 471 adult museum specimens (Fig 1, Table 1) representing four of the six extant genera of suids (Table 1): *Babyrousa* from ISEA, *Phacochoerus* and *Potamochoerus* from sub-Saharan Africa and *Sus*, from Eurasia, North Africa and ISEA. The dataset was tested for effects of sexual dimorphism but no significant variation in shape was found, so both sexes were amalgamated in all analyses.

Thirty-eight unilateral three-dimensional coordinates (Supporting Table S1) were digitised from the right side of the cranium, using a Microscribe® GLS (EMicroscribe Inc), by the first author. Specimens were standardised using Generalised Procrustes Analysis (GPA) [33] and morphological relationships explored using Principal Component Analyses (PCA) and Canonical Variance Analyses (CVA). Significance of differences in shape between groups was assessed using Multivariate Analysis of Variance (MANOVA) as well as discriminant functions with leave-one-out cross-validation. A Neighbour-Joining (NJ) tree (Fig 2) depicting the phenotypic proximity of groups was constructed from Procrustes distances between group means (Supporting Table S2). A second NJ for the same genera was generated from genetic distances derived from Gongora *et al.*'s [3] Maximum Likelihood tree based on 2 concatenated nuclear and 8 mitochondrial sequences. Analyses were conducted using MorphoJ [34], Morphologika2 [35, 36], NTSys [37], the EVAN Tool Box [38], R (version 2.13.0 R Development Core Team), and the *Morphometrics for Mathematica* package [39].

The mode of evolution in the family Suidae (i.e. the pattern of divergence resulting from long-term directional, stabilizing, or randomly varying selection [40-42]) was assessed through comparison of genetic and morphological (Procrustes) distances [40]. Distances between pairs of species were plotted on a scatter graph with genetic

distances on the x axis and Procrustes on the y. The mode of evolution was determined by assessing whether the scaling of morphological divergence is linear with respect to the genetic distances (directional or diversifying divergence); curvilinear as the square-root of genetic distance (Brownian motion); or flat (stabilizing selection or stasis), using Maximum Likelihood [42] to estimate the evolutionary mode coefficient from the following equation:

$$P = t^a$$

where P is morphological divergence, t is time since common ancestry (genetic distance serves as the proxy for this), and a is the mode coefficient ranging from 0.0 to 1.0. In a random walk process phenotypes diverge with the square root of time (0.5); in a directional process divergence is linear with time (1.0); and in perfect stasis there is no divergence with time (0.0) [40-42]. The number of independently evolving variables refers to the number of significant principal components contributing towards the Procrustes distance score.

To determine the mode of evolution responsible for the previously observed incongruence between *Potamochoerus* and *Sus*, the phylogenetic tree was projected into suid morphospace [40-43]. Cranial shape scores for species were reconstructed at the ancestral nodes of the phylogenetic tree [3] following the methodology of Martins and Hanson (see equations 4 and 5) [44], and projected into morphospace with a linear extrapolation along the branches [40]. The projections were constructed by plotting PC scores for each node and genus. The nodes were connected in order of last common ancestor and the genera to the nearest ancestral node. This generalised linear model method assumes a Brownian Motion mode of evolution and is inherently conservative.

Results – Variation in Suid Cranial Morphology

An assessment of large-scale variability in suid cranial shape using PCA (Fig 3a) revealed a morphological separation between *Phacochoerus* and *Babyrousa* at either extreme of the first principal component. Further separation of groups did not occur on any other single PC but a MANOVA based on all PC scores revealed statistically significant morphological distances between all samples in Figures 3a and 3b (Fig 3a $p < 0.0001$ $df = 4280$ $F = 2202.09$; Fig 3b $p < 0.0001$ $df = 3852$ $F = 1089.98$). The morphological distinctiveness of each species was further supported by discriminant

189 functions with cross-validation (Supporting Table S3), which correctly assigned a
190 high percentage of specimens to the correct taxon - >85%, with the exception of *S.*
191 *cebifrons* (75%) and *P. larvatus* (40% - all mismatches assigned to *P. porcus*).

192

193 The relative relationships within the main cluster of *Sus* and *Potamochoerus* (Fig 3a)
194 were illustrated using CVA (Fig 3b). CV1 separated *S. scrofa* and *Potamochoerus*
195 from *S. celebensis*, *S. philippensis* and *S. cebifrons*, while CV2 separated *S. barbatus*
196 and *S. ahenobarbus* from the other *Sus* species.

197

198 **Phylogenetic and Phenetic Relationships within Suids**

199 Fundamental differences were evident in the topologies of the NJ trees derived from
200 the genetic and morphological datasets. The genetic tree (Fig 2 left) contained two
201 monophyletic clades: the African genera *Phacochoerus* and *Potamochoerus*; and *Sus*
202 and *Babyrousa*, where *Babyrousa* was a sister taxon to *Sus*. In the morphological
203 tree (Fig 2 right) *Ph. aethiopicus* was the most morphologically distinct suid genus
204 followed by *Babyrousa*. *Potamochoerus* grouped with *S. celebensis* within the *Sus*
205 cluster. Though African pigs were genetically monophyletic, morphologically they
206 were paraphyletic.

207

208 **Mode of Evolution and Ancestral Nodes Reconstruction**

209 Figure 4a shows the results of the Maximum Likelihood estimation of the mode and
210 tempo of evolution. Points were plotted as distances between species pairs, with the
211 Procrustes distance on the y-axis and the genetic distance on the x-axis. Pairs above
212 the mode line diverged faster - given their genetic distance - than expected (i.e., there
213 is greater directional selection to make them more different), and pairs that lie below
214 the line diverged more slowly (i.e., there is greater stabilizing selection to keep them
215 from diverging). Taxon 3 (*Ph. aethiopicus*) is more divergent from all the taxa than
216 expected, signifying that directional selection has been involved sometime during its
217 evolutionary history. Taxa 1+2 and 4+5+6 (*Potamochoerus* and *Sus*) were less
218 divergent from each other than expected, suggesting that they have been influenced
219 by stabilizing selection or homoplasy.

220

221 Despite its morphological distinctiveness, taxon 7 (*Babyrousa*), was no more
222 different from any taxon (other than *Phacochoerus*) than expected given its genetic

223 distance, meaning that no special claim for directional selection was necessary. The
224 estimated mode for suids was 0.575, slightly more directional than random. The rate
225 of evolution was 0.342 Procrustes units per genetic unit (0.1), with three
226 independently evolving variables.

227

228 Figure 4b depicts the ancestral node reconstructions. Here, *Ph. aethiopicus* and
229 *Babryrousa* moved away from two clusters of *Sus* and *Potamochoerus*. *Sus* only
230 moved a short distance from the basal node, while *Potamochoerus* converged on *Sus*
231 as the nodes connecting them have wandered apart before moving closer.

232

233 **Discussion**

234 Our results demonstrate that although there is a marked discrepancy between
235 phenotypic and genotypic relationships in the Suidae, the combined signals from
236 both patterns of variability inform the evolutionary history of this group to a greater
237 degree than either dataset can demonstrate on its own.

238

239 A clear genetic monophyly was evident in the African suids (Fig 2a). This topology
240 was not recovered using phenotypic data (Fig 2b), which instead revealed a closer
241 relationship between *Potamochoerus* and *Sus* than with other sub-Saharan suid taxa.
242 Modelling the mode of evolution (Fig 4a) revealed that *Potamochoerus* cranial shape
243 was severely constrained, causing it to be less divergent from *Sus* than the model
244 would have predicted. The cause for this constraint was shown in the ancestral node
245 shape reconstruction (Fig 4b), which demonstrated that *Potamochoerus* was
246 convergent with *Sus*, thereby explaining the incongruence in the topology between
247 the genetic and morphological trees.

248

249 The similarity of form in teeth [45] and crania [5] between *Potamochoerus* and *Sus*
250 has previously been observed [3, 5], and alternatively explained as either
251 convergence[5], stasis [7], or parallel evolution [3]. The results of our ancestral node
252 reconstructions implied that *Potamochoerus* was convergent with *Sus*, and that
253 homoplasy is responsible for their morphological similarity. Since the divergence of
254 the subfamilies Phacocherinae and Suinae took place at least 7 million years ago [3],
255 the continued morphological resemblance of *Potamochoerus* and *Sus* is remarkable,

256 given their genetic differentiation, and could be indicative of similar environmental
257 adaptations.

258

259 Suids are omnivorous generalists [6], occupying a wide variety of ecosystems and
260 habitats and having a varied and flexible diet [6]. Within this family *Phacochoerus*
261 and *Babyrousa* evolved distinct cranial morphologies as a result of niche
262 specialisation [31, 46]. *Phacochoerus* are Savannah specialists with an increased
263 reliance on grazing perennial grasses over the typical suid rooting behaviour [47].
264 They have hypsodont dentition adapted towards herbivory, broad flat faces and more
265 superiorly positioned orbits [5]. Our results indicate that these specialisations
266 evolved subsequent to the last common ancestor of the African suids examined here.
267 *Babyrousa* evolved a distinct cranial morphology as a result of their extended
268 evolutionary separation and genetic isolation from other suid genera [3]. Despite
269 their unique maxillary canines (that previous studies have struggled to explain [5]),
270 our results demonstrated that the morphological divergence was no greater than
271 expected given their genetic distance from other suids.

272

273 *Sus* and *Potamochoerus* are typical suid generalists. Both genera occupy vast
274 geographic areas with highly varied habitats, and have an adaptable omnivorous diet
275 that has facilitated their success throughout their range. Our ancestral node
276 reconstruction (Fig 4b) revealed that the morphological similarity between these
277 genetically distinct genera is due to selection for the same generalist traits. Initially,
278 African suids diverged from the ancestral morphology. Despite the genetic and
279 geographic differences between *Sus* and *Potamochoerus*, the shared generalist
280 omnivorous behaviour led to a convergence in their cranial morphology despite their
281 distinct evolutionary histories.

282

283 These results resolve the incongruence between the genetics and morphology of
284 African suids. African suids are genetically monophyletic, but with a marked
285 homoplasy in cranial shape between *Potamochoerus* and *Sus*.

286

287 **Conclusion**

288 This study has demonstrated that genetic and morphological variation in suids each
289 reveal a distinct component of the evolutionary history of the family, a complete

understanding of which can only be achieved through an analysis of both. African and Eurasian suids are both genetically monophyletic. Suid morphology, however, appears paraphyletic and suggests that the sub-Saharan *Potamochoerus* is similar to Eurasian *Sus*. Cranial shape characteristics of individual genera reflect signatures derived from both their evolutionary and behavioural ancestry. Incongruence between the morphological and genetic signals can therefore reveal a more detailed appreciation of their large-scale evolutionary history. The approaches employed in this study, enabled by the recent advances in both genetic and morphological analyses, may also be used to resolve a range of similar issues in other taxonomic groups, such as the Family Rhinocerotidae [48] and the tribe Papionini [49].

Acknowledgements

This project was supported by NERC (NE/F003382/1) and The Leverhulme Trust (F/00 128/AX). We thank Frieder Mayer and Saskia Janke at the Museum für Naturkunde Berlin; Richard Sabin at the London Natural History Museum; Cécile Callou and Joséphine Lesur at Muséum National d'Histoire Naturelle, Paris; Jacqueline Studer and Manuel Ruedi at Muséum d'histoire naturelle de la Ville de Genève; Renate Schafberg at der Museum fur Haustierkunde, Halle; William Stanley of the Field Museum of Natural History; Eileen Westwig at the American Museum of Natural History; Melinda Zeder at the Smithsonian MSC, Washington DC and Alastair Macdonald at the Royal (Dick) School of Veterinary Studies for access to collections and for all their help. We also thank Thomas Cucchi, Arden Hulme-Beamen and Linus Girdland-Flink for their contributions to data collection and comments on drafts of this paper.

Bibliography

1. Oliver W. 1993 *Pigs, Peccaries and Hippos*. Gland Switzerland, IUCN.
2. Orliac M., Boisserie J.-R., MacLatchy L., Lihoreau F. 2010 Early Miocene hippopotamids (Cetartiodactyla) constrain the phylogenetic and spatiotemporal settings of hippopotamid origin. *Proceedings of the National Academy of Sciences* **107**(26), 11871-11876. (doi:10.1073/pnas.1001373107).
3. Gongora J., Cuddahee R.E., Nascimento F.F.d., Palgrave C.J., Lowden S., Ho S.Y.W., Simond D., Damayanti C.S., White D.J., Tay W.T., et al. 2011 Rethinking

- 323 the evolution of extant sub-Saharan African suids (Suidae, Artiodactyla). *Zoologica*
324 *Scripta* **40**(4), 327-335. (doi:10.1111/j.1463-6409.2011.00480.x).
- 325 4. Groves C. 2007 Current views on taxonomy and zoogeography of the genus
326 *Sus*. In *Pigs and Humans: 10,000 years of interaction* (eds. Albarella U., Dobney K.,
327 Rowley-Conwy P.), pp. 15-29. Oxford, Oxford University Press.
- 328 5. Groves C. 1981 *Ancestors for the Pigs: Taxonomy and Phylogeny of the*
329 *Genus Sus*. Canberra, Research School of Pacific Studies, Australian National
330 University.
- 331 6. Grubb P. 2005 Order Artiodactyla. In *Mammal Species of the World: a*
332 *Taxonomic and Geographic Reference* (eds. Wilson D.E., Reeder D.M.), pp. 377-
333 414, 3rd ed. Washington DC, Smithsonian Institution Press.
- 334 7. Pickford M., Morales S. 2003 New Listriodontinae (Mammalia, Suidae) from
335 Europe and a review of listriodont evolution, biostratigraphy and biogeography.
336 *Geodiversitas* **25**, 347-404.
- 337 8. Polly P.D. 2008 Developmental dynamics and G-matrices: Can
338 morphometric spaces be used to model phenotypic evolution? *Evol Biol* **35**(2), 83-96.
339 (doi:10.1007/s11692-008-9020-0).
- 340 9. Cardini A., Elton S. 2008 Does the skull carry a phylogenetic signal?
341 Evolution and modularity in the guenons. *Biological Journal of the Linnean Society*
342 **93**(4), 813-834. (doi:10.1111/j.1095-8312.2008.01011.x).
- 343 10. Caumul R., Polly P.D. 2005 Phylogenetic and environmental components of
344 morphological variation: Skull, mandible, and molar shape in marmots (Marmota,
345 Rodentia). *Evolution* **59**(11), 2460-2472. (doi:10.1111/j.0014-3820.2005.tb00955.x).
- 346 11. Hohenlohe P.A., Arnold S.J. 2008 MIPoD: A hypothesis-testing framework
347 for microevolutionary inference from patterns of divergence. *Am Nat* **171**(3), 366-
348 385. (doi:10.1086/527498).
- 349 12. Sidlauskas B. 2008 Continuous and arrested morphological diversification in
350 sister clades of characiform fishes: a phylomorphospace approach. *Evolution* **62**(12),
351 3135-3156. (doi:10.1111/j.1558-5646.2008.00519.x).
- 352 13. Carroll S.B. 2008 Evo-devo and an expanding evolutionary synthesis: A
353 genetic theory of morphological evolution. *Cell* **134**(1), 25-36.
354 (doi:10.1016/j.cell.2008.06.030).

- 355 14. Jeong S., Rebeiz M., Andolfatto P., Werner T., True J., Carroll S.B. 2008 The
356 evolution of gene regulation underlies a morphological difference between two
357 *Drosophila* sister species. *Cell* **132**(5), 783-793. (doi:10.1016/j.cell.2008.01.014).
- 358 15. Klingenberg C.P., Gidaszewski N.A. 2010 Testing and Quantifying
359 Phylogenetic Signals and Homoplasy in Morphometric Data. *Systematic Biology*
360 **59**(3), 245-261. (doi:10.1093/sysbio/syp106).
- 361 16. Salazar-Ciudad I. 2007 On the origins of morphological variation,
362 canalization, robustness, and evolvability. *Integrative and Comparative Biology*
363 **47**(3), 390-400. (doi:10.1093/icb/icm075).
- 364 17. Salazar-Ciudad I. 2008 Dealing with the conflict between developmental
365 evolutionary biology and multivariate quantitative genetics. *Evol Biol* **35**(2), 104-
366 105. (doi:10.1007/s11692-008-9022-y).
- 367 18. Agnarsson I., May-Collado L.J. 2008 The phylogeny of Cetartiodactyla: The
368 importance of dense taxon sampling, missing data, and the remarkable promise of
369 cytochrome b to provide reliable species-level phylogenies. *Mol Phylogenet Evol*
370 **48**(3), 964-985. (doi:10.1016/j.ympev.2008.05.046).
- 371 19. Hassanin A., Delsuc F., Ropiquet A., Hammer C., Jansen van Vuuren B.,
372 Matthee C., Ruiz-Garcia M., Catzeflis F., Areskoug V., Nguyen T.T., et al. 2012
373 Pattern and timing of diversification of Cetartiodactyla (Mammalia, Laurasiatheria),
374 as revealed by a comprehensive analysis of mitochondrial genomes. *Comptes Rendus*
375 *Biologies* **335**(1), 32-50. (doi:10.1016/j.crv.2011.11.002).
- 376 20. O'Leary M.A., Geisler J.H. 1999 The Position of Cetacea Within Mammalia:
377 Phylogenetic Analysis of Morphological Data from Extinct and Extant Taxa.
378 *Systematic Biology* **48**(3), 455-490. (doi:10.1080/106351599260102).
- 379 21. Thewissen J.G.M., Cooper L.N., Clementz M.T., Bajpai S., Tiwari B.N. 2007
380 Whales originated from aquatic artiodactyls in the Eocene epoch of India. *Nature*
381 **450**(7173), 1190-1194. (doi:doi.10.1038/nature06343).
- 382 22. O'Leary M.A., Gatesy J. 2008 Impact of increased character sampling on the
383 phylogeny of Cetartiodactyla (Mammalia): combined analysis including fossils.
384 *Cladistics* **24**(4), 397-442. (doi:10.1111/j.1096-0031.2007.00187.x).
- 385 23. Price S.A., Bininda-Emonds O.R.P., Gittleman J.L. 2005 A complete
386 phylogeny of the whales, dolphins and even-toed hoofed mammals (Cetartiodactyla).
387 *Biological Reviews* **80**(03), 445-473.

- 388 24. Boisserie J.-R., Lihoreau F., Brunet M. 2005 The position of Hippopotamidae
389 within Cetartiodactyla. *Proc Natl Acad Sci U S A* **102**(5), 1537-1541.
390 (doi:10.1073/pnas.0409518102).
- 391 25. Boisserie J.-R., Fisher R.E., Lihoreau F., Weston E.M. 2011 Evolving
392 between land and water: key questions on the emergence and history of the
393 Hippopotamidae (Hippopotamoidea, Cetancodonta, Cetartiodactyla). *Biological*
394 *Reviews* **86**(3), 601-625. (doi:10.1111/j.1469-185X.2010.00162.x).
- 395 26. Geisler J.H., Theodor J.M. 2009 Hippopotamus and whale phylogeny. *Nature*
396 **458**(7236), E1-E4.
- 397 27. Naylor G.J.P., Adams D.C. 2001 Are the Fossil Data Really at Odds with the
398 Molecular Data: Morphological Evidence for Cetartiodactyla Phylogeny
399 Reexamined. *Systematic Biology* **50**(3), 444-453. (doi:10.1080/10635150118184).
- 400 28. Larson G., Dobney K., Albarella U., Fang M.Y., Matisoo-Smith E., Robins
401 J., Lowden S., Finlayson H., Brand T., Willerslev E., et al. 2005 Worldwide
402 phylogeography of wild boar reveals multiple centers of pig domestication. *Science*
403 **307**(5715), 1618-1621. (doi:10.1126/science.1106927).
- 404 29. Mona S., Randi E., Tommaseo-Ponzetta M. 2007 Evolutionary history of the
405 genus *Sus* inferred from cytochrome b sequences. *Mol Phylogenet Evol* **45**(2), 757-
406 762. (doi:10.1016/j.ympev.2007.05.025).
- 407 30. Oliver W., Leus K. 2008 *Sus scrofa*. IUCN. IUCN Red List of Threatened
408 Species. www.iucnredlist.org.
- 409 31. Grubb P. 1993 *The Afrotropical Suids Phacochoeris, Hylochoerus and*
410 *Potamochoerus: taxonomy and distribution*. . Cornell University, IUCN.
- 411 32. Lucchini V., Meijaard E., Diong C.H., Groves C.P., Randi E. 2005 New
412 phylogenetic perspectives among species of South-east Asian wild pig (*Sus* sp.)
413 based on mtDNA sequences and morphometric data. *J Zool* **266**, 25-35.
414 (doi:10.1017/s0952836905006588).
- 415 33. Mitteroecker P., Gunz P. 2009 Advances in Geometric Morphometrics. *Evol*
416 *Biol* **36**(2), 235-247. (doi:DOI 10.1007/s11692-009-9055-x).
- 417 34. Klingenberg C.P. 2008 Morphoj. Faculty of Life Sciences.
418 http://www.flywings.org.uk/MorphoJ_page.htm.
- 419 35. O'Higgins P., Jones N. 2006 Tools for statistical shape analysis. Hull York
420 Medical School. <http://sites.google.com/site/hymsfme/resources>.

- 421 36. O'Higgins P., Jones N. 1998 Facial growth in *Cercocebus torquatus*: an
422 application of three-dimensional geometric morphometric techniques to the study of
423 morphological variation. *Journal of Anatomy* **193**, 251-272. (doi:10.1046/j.1469-
424 7580.1998.19320251.x).
- 425 37. Rohlf F.J. 2008 NTSYSpC: Numerical Taxonomy System. Exeter Publishing,
426 Ltd.
- 427 38. EVAN toolkit 2010 <http://evan-society.org/node/42>
- 428 39. Polly P.D. 2012 Morphometrics for Mathematica, Version 8.6.2. Indiana
429 University. <http://mypage.iu.edu/~pdpolly/Software.html>. .
- 430 40. Polly P.D. 2008 Adaptive Zones and the Pinniped Ankle: A 3D Quantitative
431 Analysis of Carnivoran Tarsal Evolution. In *Mammalian Evolutionary Morphology:
432 A Tribute to Frederick S Szalay* (eds. Sargis E., Dagosto M.), pp. 167-196.
433 Dordrecht, The Netherlands, Springer.
- 434 41. Polly P.D. 2004 On the simulation of the evolution of morphological shape:
435 multivariate shape under selection and drift. *Palaeontologia Electronica* **7.2.7A**, 28.
- 436 42. Gomez-Robles A., Polly P.D. 2012 Morphological Integration in the
437 Hominin dentition: Evolutionary, Developmental, and Functional Factors. *Evolution*
438 **66**(4), 1024-1043. (doi:10.1111/j.1558-5646.2011.01508.x).
- 439 43. Rohlf J. 2002 Geometric morphometrics and phylogeny In *Morphology,
440 Shape and Phylogeny* (eds. MacLeod N., Forey P.L.), pp. 175-193, CRC Press.
- 441 44. Martins E.P., Hansen T.F. 1997 Phylogenies and the Comparative Method: A
442 General Approach to Incorporating Phylogenetic Information into the Analysis of
443 Interspecific Data. *The American Naturalist* **149**(4), 646-667.
- 444 45. Janis C.M. 1997 Ungulate teeth, diets, and climate changes at the
445 Eocene/Oligocene boundary. *Zoology - Analysis of Complex Systems* **100**, 203-220.
- 446 46. Grubb P. 1993 *Eurasian Suids Sus and Babyrousa*. Cornell University,
447 IUCN.
- 448 47. Estes R. 1991 *The Behavior Guide to African Mammals, Including Hoofed
449 Mammals, Carnivores, Primates*. Los Angeles, University of California Press.
- 450 48. Willerslev E., Gilbert M.T.P., Binladen J., Ho S.Y.W., Campos P.F., Ratan
451 A., Tomsho L.P., da Fonseca R.R., Sher A., Kuznetsova T.V., et al. 2009 Analysis of
452 complete mitochondrial genomes from extinct and extant rhinoceroses reveals lack
453 of phylogenetic resolution. *BMC Evolutionary Biology* **9**. (doi:10.1186/1471-2148-9-
454 95).

455 49. Gilbert C.C. 2011 Phylogenetic analysis of the African papionin basicranium
 456 using 3-D geometric morphometrics: The need for improved methods to account for
 457 allometric effects. *American Journal of Physical Anthropology* **144**(1), 60-71.
 458 (doi:10.1002/ajpa.21370).

459
 460

Genus	Species	Common Name	Range	Sample Size
<i>Porcula</i>	<i>P. salvania</i>	Pygmy hog	Assam, India Sub-Saharan	*
<i>Phacochoerus</i>	<i>P. africanus</i>	Warthog	Africa Sub-Saharan	11
<i>Potamochoerus</i>	<i>P. larvatus</i>	Bushpig	Africa Sub-Saharan	6
<i>Potamochoerus</i>	<i>P. porcus</i>	Red River Hog	Africa Sub-Saharan	11
<i>Hylochoerus</i>	<i>H. meinertzhageni</i>	Forest Hog	Africa	*
<i>Babyrhousa</i>	<i>B. celebensis</i>	Babirusa	North Sulawesi	20
<i>Sus</i>	<i>S. barbatus</i>	Bornean bearded pig	Borneo	19
<i>Sus</i>	<i>S. ahonebarbus</i>	Palawan bearded pig	Palawan Negros,	4
<i>Sus</i>	<i>S. cebifrons</i>	Visayan Warty Pig	Philippines	6
<i>Sus</i>	<i>S. philippensis</i>	Philippine Warty Pig	Philippines	26
<i>Sus</i>	<i>S. scrofa</i>	Wild Boar	Eurasia	329
<i>Sus</i>	<i>S. verrucosus</i>	Javan Warty Pig	Java	*
<i>Sus</i>	<i>S. celebensis</i>	Celebes Warty Pig	Sulawesi	39

461

462 **Table 1:** List of currently recognised suid taxa⁴, those marked* are not represented
 463 in the analysis. Sample size refers to numbers of individuals of each genus (total 471)
 464 used in this study.

465

466 **Figure 1:**

467 Map showing distribution of samples. Circle size on the map corresponds to sample
468 size. Colours correspond to species.

469

470 **Figure 2:**

471 Genetic (left) and morphological (right) NJ trees. Colours correspond those in Figure
472 1. The red boxes highlight the position of *Sus* and the green boxes the position of the
473 African suids. Further information about group size and location can be found in
474 Figure 1 and Table 1.

475

476 **Figure 3:**

477 Figure 3a: PCA: PC1 vs PC2 Figure 3b: CVA: CV1 vs CV2 of the *Sus* and
478 *Potamochoerus* group with representations of the average morphology of the main
479 species analysed.

480 Colours correspond to those in the map in Figure 1.

481

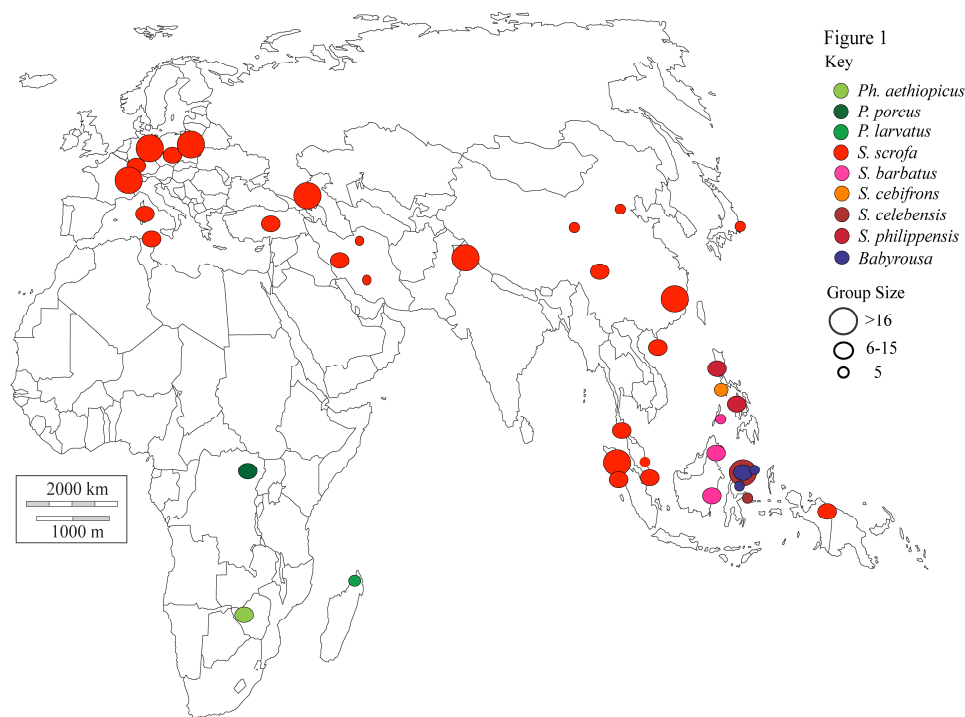
482 **Figure 4:**

483 Maximum Likelihood estimate of the tempo and mode of evolution in suids (4a) and
484 ancestral node reconstructions of PC1 and PC2 (4b). Ancestral node scores are
485 shown in green, with the basal node in black, the position of genus is shown in red.

486 For further explanation see text.

487

488 **Figure 1**

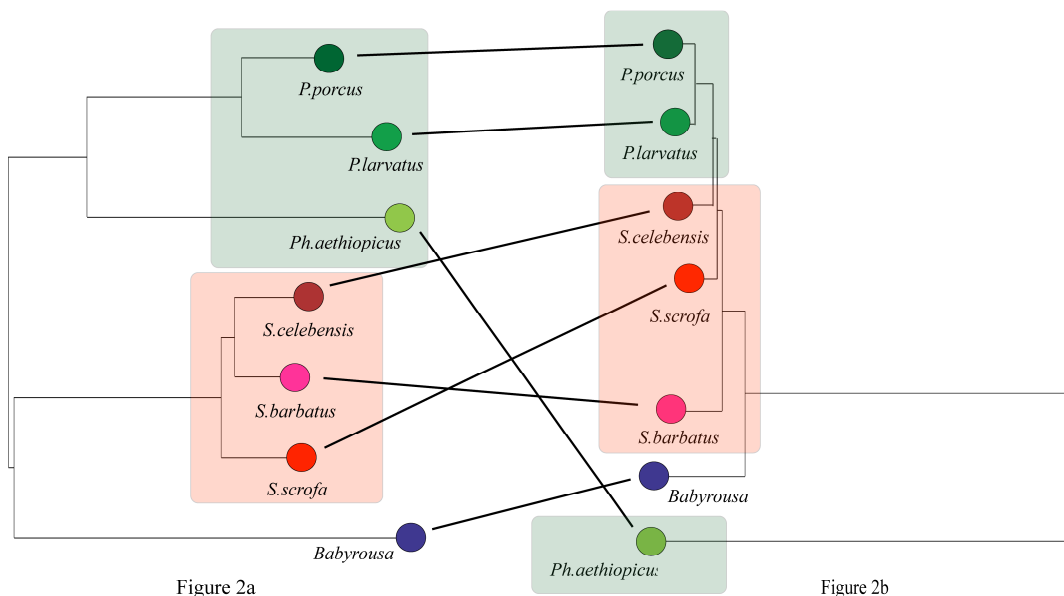


489

490

491

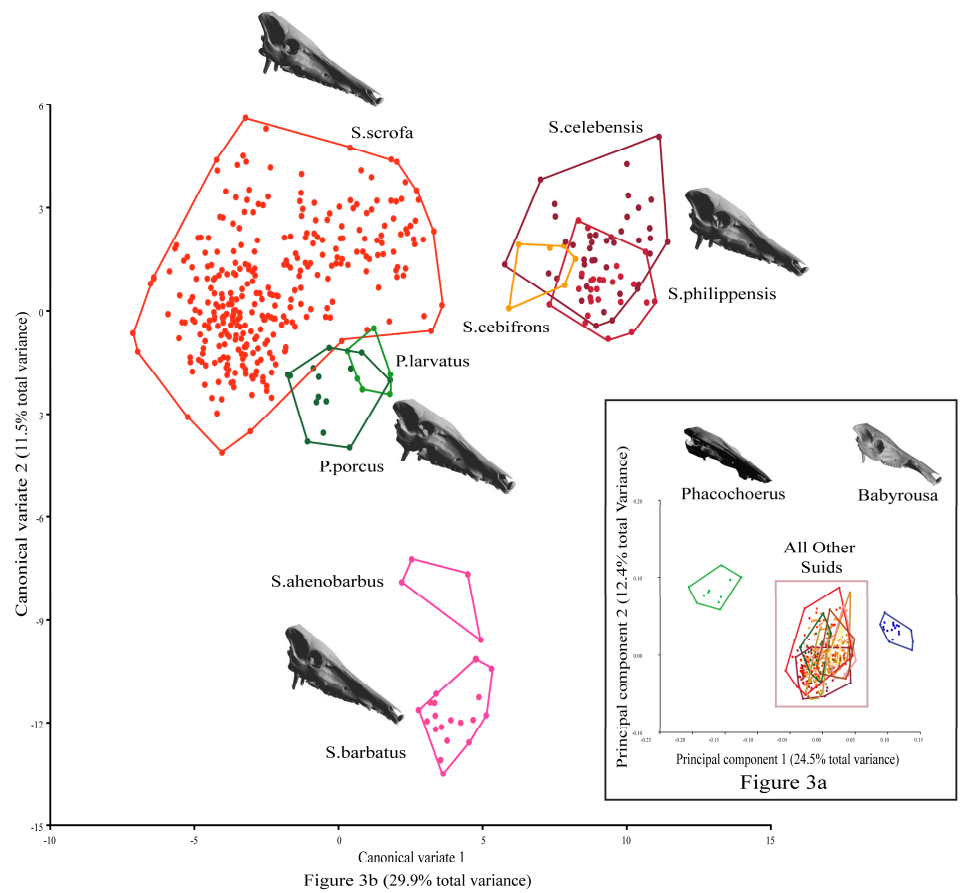
492 **Figure 2**



493

494

495



497

498

499 **Figure 4**

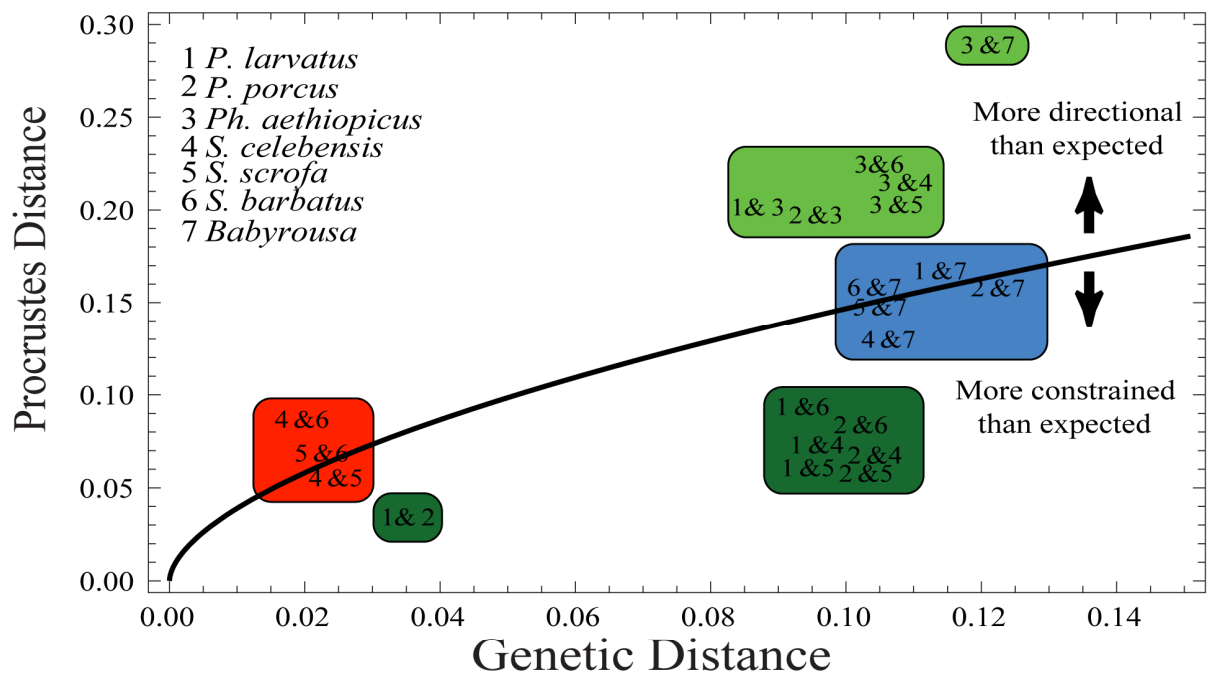


Figure 4a

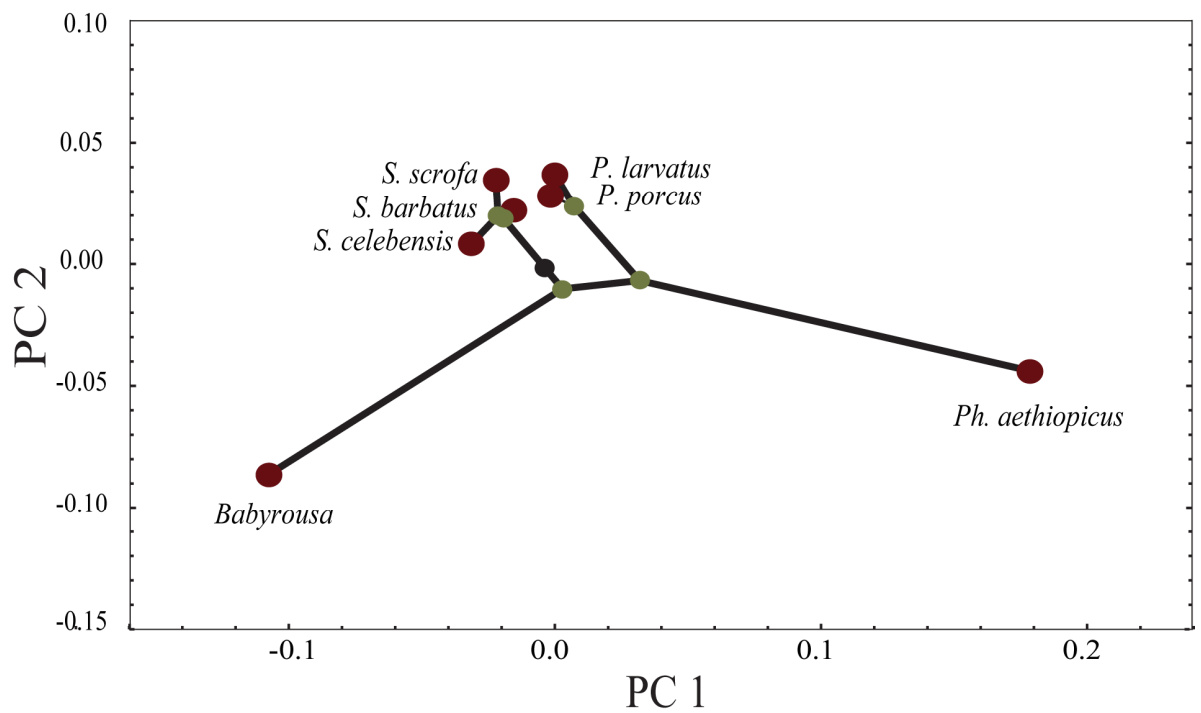


Figure 4b

500

501

502	S1: List of Landmarks	
503	1	Most anterior midline point on nasals
504	2	Anterior join in nasal and pre maxilliar suture
505	3	Anterior point of nasal
506	4	Suture at the meeting point of the premaxillar, maxillar and nasal
507	5	Most posterior point of superorbital foramen and groove
508	6	Most lateral point of the Nuchal Crest
509	7	Most anterior point of Nuchal Crest - on the midline of the parietal
510	8	Most superior point of zygomatic process of temporal
511	9	Most posterior point of zygomatic process of malar
512	10	Superior point of the temporal process of malar
513	11	Most inferior point of the malar (zygomatic arch)
514	12	Anterior most point of the process emerging of the malar (zygomatic arch)
515	13	Most posterior point of infraorbital foramen
516	14	Most anterior point of infraorbital foramen
517	15	Most superior point of the lower lacrimal foramina
518	16	Most superior point of the occipital
519	17	Most inferior point of the occipital
520	18	Base of supraorbital process
521	19	Anterior point of incisive foramen/palatine fissure
522	20	Posteriormost point of incisive foramen/palatine fissure
523	21	Most anterior point of canine alveolus
524	22	Most posterior point of canine alveolus
525	23	Anterior point of the alveolar margin of the tooth row
526	24	Contact points between M3/M2, projected labially (buccially) onto alveolar
527	margin	
528	25	Most posterior point of the alveolar margin of the tooth row
529	26	Contact points between M3/M2, projected lingually onto alveolar margin
530	27	Most anterior point of the pterygoid process of the palatine
531	28	Most lateral point of the pterygoid process of the palatine
532	29	Most posterior point of the pterygoid process of the palatine
533	30	Suture of the nasal and palatine bones (on the midline)
534	31	Tip of posterior nasal spine
535	32	Meeting point between the basisphenoid and basioccipital along midline,
536	posterior of the vomer	
537	33	Anterior most point of the bulla tympanica
538	34	Most anterior point of the paramastoid process
539	35	Most anterior point on the margin of the Hypoglossal canal
540	36	Lowest point on the orobasal border of foramen magnum
541	37	Most posterior tip of occipital condyle
542	38	Most superior point on the border of foramen magnum
543		

544
545

Table S2
Distance Matrix of procrustes distances between taxa in Figure 2b

	<i>S.scrofa</i>	<i>S.celebensis</i>	<i>Babyrousa</i>	<i>Phacochoerus</i>	<i>P.larvatus</i>	<i>P.porcus</i>	<i>S.barbatus</i>
<i>S.scrofa</i>	0						
<i>S.celebensis</i>	0.0617	0					
<i>Babyrousa</i>	0.1497	0.1304	0				
<i>Phacochoerus</i>	0.8473	0.8667	0.8797	0			
<i>P.larvatus</i>	0.0747	0.0754	0.1658	0.8602	0		
<i>P.porcus</i>	0.0617	0.0601	0.1564	0.8591	0.0346	0	
<i>S.barbatus</i>	0.0684	0.0893	0.1596	0.8544	0.0949	0.0853	0

Table S3
Discriminant function cross validation scores - % of species correctly assigned

Species	% Correctly Assigned	
<i>S.scrofa</i>	99.10%	
<i>Babirusa</i>	100.00%	
<i>S.ahonebarbus</i>	75.00%	Mismatch assigned to <i>S.barbatus</i>
<i>S.cebifrons</i>	66.67%	
<i>S.celebensis</i>	89.74%	
<i>S.philippensis</i>	85.19%	
<i>S.barbatus</i>	94.74%	
<i>Phacochoerus</i>	100.00%	
<i>P.porcus</i>	85.71%	
<i>P.larvatus</i>	50.00%	Note - all mismatches assigned to <i>P.porcus</i>

546
547

1

2

3

4

5

6

7

Chapter 4

8

Manuscript 2

9

10 **Pigs in Space: Biogeographic variation in *Sus scrofa***

11

12

13 **Pigs in Space: Biogeographic variation in *Sus scrofa***

14 Target Journal: Journal of Biogeography

15

16 Joseph OWEN^{a,b}, Allowen EVIN^{c,d}, Keith DOBNEY^c, Thomas CUCCHI^{c,d}, Peter
17 ROWLEY-CONWY^a, Greger LARSON^a and Una STRAND VIDARSDOTTIR^b.

18

19 ^aDepartment of Archaeology, University of Durham, South Road, Durham DH1 3LE,
20 United Kingdom. J.t.d.owen@durham.ac.uk; p.a.rowley-conwy@durham.ac.uk;
21 greger.larson@durham.ac.uk.

22 ^dDepartment of Anthropology, University of Durham, South Road, Durham DH1
23 3LE, United Kingdom. una.vidarsdottir@durham.ac.uk

24 ^cDepartment of Archaeology, University of Aberdeen, St.Mary's Building,
25 Elphinstone Road, United Kingdom. a.evin@abdn.ac.uk; keith.dobney@abdn.ac.uk .

26 ^dCNRS-Muséum National d'Histoire Naturelle, UMR 7209, Archéozoologie,
27 histoire des sociétés humaines et de peuplements animaux, 55 rue Buffon, 75005
28 Paris, France. evin@mnhn.fr; cucchi@mnhn.fr.

29

30 **Abstract**

31 Pigs have one of the widest distributions of any large mammal, endemic throughout
32 the Palaearctic and Indomalaya. Throughout this range there are recognised
33 morphotypes that have traditionally been described as separate species, mainly on the
34 basis of size and morphological characteristics. These methods are also the basis of
35 investigations into the species history, including studies of domestication. However
36 most of these studies fail to appreciate all the sources of possible variation present
37 within these measurements beyond sexual diamorphism. It has long been recognised

38 that climate, latitude and longitude cause shape and size changes in large mammals.
39 The impact that these variables have on suid morphology have not been
40 systematically quantified in suids across their natural range, recent advances in shape
41 analysis, especially in geometric morphometrics (GMM), make this possible. Here
42 we apply GMM to 429 adult suid crania, including most genera, but concentrating on
43 the most wide spread genus, *Sus scrofa*. Our results demonstrate that environmental
44 and climatic variables are major sources of variation in both cranial shape and size in
45 *Sus scrofa*, with precipitation strongly linked to size change in European pigs. The
46 effect of environmental and geographic variables diminishes as wider geography
47 regions and more species are included, the remaining variance increases,
48 representing factors not tested including genetic variation that could be interpreted as
49 speciation.

50

51 **Introduction**

52 The wild boar (*Sus scrofa* L.1758) occurs naturally throughout the Palaearctic and
53 Indomalaya including Island South East Asia (ISEA), and is present but non-native
54 to the Americas and Australasia (Murray, 1978). As such it has one of the largest
55 ranges of any extant large mammals, occupying a generalised omnivorous niche in
56 many varied and differing habitats (Oliver and Leus, 2008). The pig is important to
57 humans as a food source, both in its domesticated form (Oliver and Leus, 2008) and
58 in its wild state as a game animal (Scandura et al., 2011) and has been intensively
59 studied, focusing both on its history and interaction with humans (e.g. the origins and
60 processes of domestication (Albarella et al., 2007, Rowley-Conwy et al., 2012), and
61 speciation (Groves, 1981, Genov, 1999) .The pig is unusual both in the breadth of its
62 natural range (Oliver and Leus, 2008) and its strong phylogeographic structure

63 (Larson et al., 2005). The implications of natural variation across its range are rarely
64 factored into research, yet greater understanding of morphological variation in the
65 wild could have an important impact on the understanding of morphological
66 variation caused by domestication or speciation. This paper considers the role that
67 natural variation, due to geography or environmental factors, plays in cranial
68 morphological variation of *Sus scrofa* and other *Sus* species.

69

70 **Geography, climate and other causes of shape change**

71 The relationship between environment and geography on the one hand, and
72 phenotypic variability on the other is well established in other mammal species with
73 extensive distributions such as Reindeer (*Rangifer tarandus*) and Dogs (*Canis lupus*
74 *familiaris*) (Cardini et al., 2007, Millien et al., 2006, Albarella et al., 2009,
75 Weinstock, 2000). Size is known to be strongly correlated with temperature under
76 what is known as ‘Bergman’s Rule’ where organisms have larger body size under
77 colder climatic conditions (Meiri and Dayan, 2003). This is often interpreted as
78 latitudinal variation within species, as temperature is highly correlated with latitude
79 (thus latitude is then used as a proxy for temperature) and a positive correlation with
80 latitude and body size has been documented among most endotherms (Meiri and
81 Dayan, 2003). Indeed, Bergman’s rule holds true for 62%-83% of vertebrate species
82 excluding squamates and fish (where it is closer to ~30% of species) (Millien et al.,
83 2006). The most widely given explanation of Bergman’s rule is thermal regulation,
84 where there is a selective advantage to a higher body surface-to-volume ratio in
85 warm regions and a lower surface-to-volume ratio in colder areas (Mayr, 1954). This
86 has been questioned as there are more efficient methods of body temperature control
87 (e.g. fur insulation (Scholander, 1955, 1956), and body size often correlates better or

88 more strongly in combination with other environmental factors such as moisture
89 availability (Millien et al., 2006).

90

91 Moisture (or precipitation) also influences size and morphology, as moisture is often
92 a limiting factor of primary productivity, especially in arid and semi-arid
93 environments (Yom-Tov and Geffen, 2006). Primary productivity has been linked to
94 mammalian body size (Millien et al., 2006); it is also an important factor in diet
95 (Birkhofer and Wolters, 2012) which in turn has an impact on morphology. The
96 effect of diet on cranial morphology has been studied through biomechanics (Herring
97 et al., 2001, van Cakenberghe et al., 2002) which in pigs has focused on the muscles
98 associated with mastication in wild and domestic *Sus scrofa* (Dinu, 2009, Herring et
99 al., 2001). Mastication is a forceful cranial activity that produces strain loads on
100 craniofacial bone; the coarser the diet, the greater the work load associated with
101 breaking it down and the larger the muscles required to do so. In response to this, and
102 in accordance with Wolff's law (Wolff, 1986) which generally states, bone remodels
103 to become more robust in response to increased strain loads. *Sus scrofa* inhabits a
104 large variety of habitats and has a very broad diet (Oliver and Leus, 2008) which
105 could have an obvious impact on cranial shape. Pigs are also noted for their rooting
106 behaviour, digging with their snouts for roots, tubers and truffles (Massei and Genov,
107 2004). Animals that undertake a greater proportion of rooting as a food gathering
108 activity will have greater developed muscles around the nasal bone, impacting on the
109 shape of the front of the cranio-facial area (Sack, 1982).

110

111 Body size and insularity, or the 'island rule', dictates that among mammals and birds
112 small animals get larger and larger animals get smaller (Meiri et al., 2011). Reasons

113 for this can include absence/reduction of predators and competitors, as well as
114 resource and space limitations (Millien et al., 2006). It has been suggested that the
115 “island rule” corresponds to a clade-specific response to insularity instead of a size
116 related phenomenon (Meiri et al., 2006, Meiri, 2008). As with any rule there are
117 exceptions, e.g. carnivores are more dependent on prey availability than influenced
118 by insularity (Meiri et al., 2005). Although insularity has recently been shown to
119 occur less often than previously been thought (Meiri et al., 2011) it does hold true (in
120 the form of dwarfism) in large species.

121

122 There have been few studies into the effect of environmental pressure on cranial
123 morphological variation outside humans (Cardini & Elton 2007), and little in pigs to
124 date (Fuller, 1965, Larsson et al., 2005). Those that have been carried out have
125 mainly focused on primates (Cardini et al., 2007, Viguier, 2002) with only a few
126 studies on other animals such as the Tammar Wallaby (*Macropus eugenii*) (Hadley et
127 al., 2009), these have shown that cranio-facial variation is strongly linked to
128 environmental and geographic factors. The interactions between climatic factors such
129 as moisture and temperature are difficult to untangle, as these factors tend to co-vary,
130 although several studies have done so through differing approaches based on
131 regression (Cardini et al., 2007, Yom-Tov and Geffen, 2006).

132

133 **Known constraints on *Sus scrofa* range**

134 Although *Sus scrofa* is found in a wide variety of habitats it cannot tolerate sustained
135 temperatures above 35°C (95°F) with humidity above 65% without adequate water or
136 shade, this intolerance is known mainly through transportation of domestic livestock
137 and is due to a lack of sweat glands and thick layers of subcutaneous fat (Hafez,

138 1968). Alleviation of high temperatures in the wild is achieved through seeking
139 shade and wallowing in mud or water, thus wild pigs are rarely found far from water
140 and shade (Oliver, 1993) even in semi-arid environments. The main mechanism of
141 population regulation is intra-specific competition for food or space governed by
142 stochastic environmental factors (Uzal and Nores, 2004). This is reflected in the
143 preference of *S.scrofa* to inhabit areas of energy rich foods (Massei and Genov,
144 2004). In this investigation we will use rainfall (or moisture) as a proxy for primary
145 productivity (and thus diet) to investigate its potential impact on cranial morphology.

146

147 **Known biogeographic variation within *Sus scrofa***

148 Across the extensive natural range of *S.scrofa* there are various morphologies that
149 have been split into 4 main groupings; the ‘Western races’ of Europe, North Africa
150 and the Middle East; the ‘Indian races’ from Eastern Iran to Thailand; the ‘Eastern
151 races’ of Mongolia and Russia to China and Vietnam; and the ‘Indonesian races’
152 from the Malay peninsula through the Indonesian islands (Groves, 1981, Groves,
153 2007, Grubb, 1993). These racial groupings fit tolerably well with the known
154 mitochondrial phylogeny of *Sus* (e.g. Larson et al. (2005)) which shows separate
155 maternal lineages in the geographic regions proposed by studies on morphology
156 (Reproduced in figure 1).

157

158 Known variation across Eurasia includes size increases from West to East and South
159 to North, with larger individuals in Eastern Europe and the Near East, and smaller
160 pigs in Western and Southern Europe (Albarella et al., 2009). There are also
161 incidences of insular dwarfism e.g. on Corsica and Sardinia (Albarella et al., 2009) as
162 well as in ISEA (e.g. *Sus ahonobarbus*, (Oliver, 2010). Size increases in Eastern

163 Eurasia have been attributed to ‘continentality’ i.e. harsher winters in the East having
164 an increased bottlenecking effect reducing intraspecific competition. The South-
165 North size increase is driven, and explained by, the presence of large boar in the Near
166 East (Albarella et al., 2009, Weinstock, 2000), leading Albarella et al. (2009) to
167 conclude that pigs exhibit an inverse relationship of body size and temperature.

168

169 Davis (1981) surveyed extant and past pig populations (amongst other animals such
170 as aurochs, dogs, foxes, gazelles and goats) in the Levant, discovering a negative
171 temperature-size relationship in modern populations coupled with size decreases in
172 pigs at the end of Pleistocene and another size decrease associated with
173 domestication. Davis attributed size decreases to Bergman’s rule in wild pigs, foxes
174 and dogs, noting that the regression lines of log dental size on temperature are similar
175 in these species. The Pleistocene size reduction (present in all the animals Davis
176 examined) is explained by the end of the last glacial maximum which occurred at the
177 Pleistocene/Holocene transition.

178

179 Studies of pig cranial morphology that do exist are limited either by approach (e.g. to
180 speciation studies e.g. (Groves, 1981, 2007, Genov, 1999, Lucchini et al., 2005) or to
181 specific geographic areas (Albarella et al., 2009, Endo et al., 2002, Alves et al.,
182 2010). Genetic studies of Suid populations have been more encompassing, with
183 several family-wide phylogenies published (e.g. (Gongora et al., 2011, Mona et al.,
184 2007), but only Larson et al., (2005) examined the phylogeography of *Sus*, by
185 conducting a global investigation into the structure of mitochondrial DNA whilst
186 looking for evidence of centres of domestication. They showed that pigs, and

187 especially *Sus scrofa*, have a strong geographic basis of genetic partition (see Figure
188 1).

189

190 We propose to investigate biogeographic signals in *Sus scrofa* cranial morphology
191 using a Geometric Morphometric approach. *Sus scrofa* was chosen as the focus of
192 the investigation as it is the most widely spread species of suid and the only one that
193 inhabits multiple habitat types. We first test the long standing hypothesis that *Sus* and
194 *Sus scrofa* cranial morphology co-varies with geography or climate, and if it does –
195 to what degree climate and geography explains suid cranial variation. We also
196 examine our data for any affects of insularity. Finally we compare phylogeography to
197 phenotypic variation, investigating whether the traditional taxonomy is congruent
198 with the mitochondrial distribution map of *Sus*.

199

200 **Materials**

201 The sample analysed consists of 334 modern *Sus scrofa* crania from museum
202 collections; representing a large part of the geographic distribution of the species.
203 The composition of the sample and the geographic and environmental covariates
204 used in analysis can be found in Table 1. For comparative analysis with the wider
205 genus *Sus* we added 95 specimens from other genera, which are also listed in Table
206 1.

207

208 Geographic and environmental covariates used were latitude, longitude, elevation (in
209 metres above sea level), mean average annual temperature (degrees Celsius) and its
210 standard deviation (SD), mean annual precipitation (millimetres) with associated
211 standard deviation and the Shannon index of precipitation, a diversity index

212 reflecting seasonal variation in precipitation (Bronikowski and Webb, 1996).
213 Geographic co-ordinates for latitude and longitude were extrapolated from museum
214 data, specimens were grouped (see table 1) according to location as many samples
215 had insufficient data to pin-point exact individual origins. These groups were
216 collated into regions to assess possible wider bio-geographic structuring: Europe, the
217 Near East, Mainland Asia and Island South East Asia (ISEA), as based on prior
218 studies of biogeographic structuring in *S.scrofa* (Groves 1981). Elevation
219 information for geographic co-ordinates originates from the SRTM3 database, a
220 NASA global survey taken from the GPS visualizer website (Schneider 2010).
221 Temperature and precipitation data were extrapolated from the Willmott and
222 Matsuura data base (Legates & Willmott, 1990a,b; Willmott & Feddema, 1992;
223 Willmott & Matsuura, 2001). Environmental data were generated for the geographic
224 group mean latitude and longitude rather than individual samples; thus analyses
225 conducted using geographic or environmental covariates are based on variables
226 generated for the mean group location (given in table 1).
227

Group Name (*)	Locality	Group Size	Mean Centroid Size	DF %	Longitude (°)	Latitude (°)	Elevation (m)	Mean Temperature (Celsius)	SD of temp	Monthly Rainfall (mm)	SD of monthly rainfall	Shannon Index
S.s.Geneva (E)	Region from Saillenard, France to Geneva, Switzerland	33	608.72	72.73	5.37	46.70	200	11.02	6.46	938	10.93953	0.996342
S.s.SWGermany (E)	Heilbronn	13	593.1	53.85	9.19	49.19	188	9.33	6.71	745.8	8.557559	0.996498
S.s.Sardinia (E)	San Nicolò Gerrei	16	513.02	100	9.32	39.53	387	14.68	6.47	753.6	34.19213	0.933188
S.s.Tunis (E)	Tunis, Tunisia	10	657.59	60	10.11	36.48	240	20.99	1.32	1707.9	136.7352	0.810651
S.s.Berlin (E)	Zoological gardens, Berlin	32	660.3	46.8	12.79	52.57	37	8.82	6.95	510.6	8.361546	0.992621
S.s.SWPoland (E)	Zabkowice	16	600.65	37.50	16.93	50.68	268	7.89	7.05	693.4	20.68701	0.976625
S.s.EPoland (E)	Nowa Wieś, N. Warsaw	28	634.43	67.86	21.11	52.53	82	7.97	7.93	518.3	17.36525	0.971867
S.s.WRussia (E)	Dubroŭna, Belarus	6	647.34	16.67	30.77	54.44	215	5.28	9.05	545.3	19.55907	0.968689
S.s.Turkey (NE)	Cihanbeyli	8	687.41	37.5	32.68	38.77	1138	9.90	7.97	412.9	15.78281	0.952314
S.s.Caucasus (NE)	Dagestan	20	762.7367	60	46.60	43.10	514	11.87	9.47	397.9	10.29046	0.982501
S.s.IraqIran (NE)	Sedeh Lenjan, Iran	9	718.19	55.56	51.26	32.20	2158	21.87	8.93	266.8	24.8564	0.747114
S.s.NEIran (NE)	Estakhr Sar (Nr. Parvar Protected area)	7	677.12	60	53.38	36.18	985	13.59	7.14	712.1	24.63562	0.964516
S.s.SIran (NE)	Rafsanjan, Iran	5	661.42	20	55.71	30.64	1408	17.64	9.23	79.6	6.8488	0.791566

S.s.Fukien (Asia)	China - Fukien	13	578.34	61.54	119.3	26.07	9	17.09	6.66	1409.9	62.41051	0.944027
S.s.Szechuan (Asia)	China - Szechuan	10	605.81	30	103	30	593	16.43	6.86	1464.2	115.1128	0.843593
S.s.Hainan (Asia)	China - Hainan	3	473.6	0	109.95	19.17	262	24.08	3.67	1409.3	83.06781	0.901374
S.s.Shanxi (Asia)	China - Shanxi	7	615.99	57.14	112	38	1165	5.30	11.03	432.6	41.99508	0.784594
S.s.Gansu (Asia)	China - Gansu	4	545.35	25	102.3	38	1938	5.49	10.34	303.3	24.76137	0.808421
S.s.Burma (Asia)	Tenasserim	13	554.52	53.85	98.75	13	3625	25.25	1.11	3209.9	285.5248	0.771156
S.s.India (Asia)	Kashmir	18	624.32	55.56	76	34.5	4092	-3.30	10.87	494.7	28.74386	0.914863
S.s.Japan (Asia)	Tokyo	6	627.74	100	139.715	35.42	241	15.69	7.88	1706.8	58.33831	0.969076
S.s.Malaysia (ISEA)	Johor	7	584.33	57.14	103.5	1.49	13	26.77	0.40	2834.4	49.77332	0.991811
S.s.Papua (ISEA)	South Eastern Irian Jaya	9	528.35	88.89	140.71	-2.53	178	28.23	0.21	2384.9	66.48296	0.980097
S.s.Nsumatra ISEA)	North Sumatra Prov.	23	513.06	69.57	99.00	2.00	1024	19.28	0.17	2338.9	54.3692	0.984596
S.s.Ligga Is. (ISEA)	Lingga archipelagos (Sumatra)	7	519.82	42.86	104.00	1.04	17	26.28	0.35	2897.9	50.76103	0.99205
S.s.Nias Is. (ISEA)	Nias (Sumatra)	6	499.12	66.67	97.53	1.10	82	26.73	0.39	3452.7	78.47157	0.986677
S.ahonebarbus	Palawan	4	542.03		118.40	9.53	264	22.23	0.48	1868	78.00795	0.945146
S.b.Borneo	Borneo	12	719.79		116.83	-1.36	0	26.92	0.27	2371.3	30.35093	0.995525
S.b.Malay	Malaysia	7	685.84		117.54	4.42	14	26.40	0.29	1875.6	33.80863	0.990953
S.ceb	Negros	6	455.98		123.00	10.00	710	26.74	0.69	2115.7	67.00471	0.970456
S.cel.Peleng	Peleng Island	6	462.5		123.17	-1.40	11	25.33	0.33	1812.4	66.04734	0.966151
S.cel.Lembbeh	Lembbeh (N.Sul)	5	422.48		125.23	1.43	172	27.55	0.34	2455.5	67.76733	0.978

S.cel.Bumbulan	Bumbulan (N.Sul)	28	460.19		121.94	0.47	19	21.84	0.25	2429.7	41.63954	0.992479
S.p.Mindanao	Mindanao	12	508.5		125.00	8.00	664	24.63	0.51	2807.9	85.55993	0.973708
S.p.Luzon	Luzon	14	511.04		121.00	16.00	413	21.44	1.24	2122.2	101.0302	0.936081

Table 1: Group information and covariates: Data was collected from Museum für Naturkunde (Berlin, Germany), London Natural History Museum (UK), Muséum d'histoire naturelle de la Ville de Genève (Switzerland), Museum für Haustierkunde, (Halle, Germany), Field Museum of Natural History (Chicago, USA), American Museum of Natural History (NY, USA), Smithsonian MSC (Washington DC, USA).

DF% = percent of group correctly assigned in discriminant function analysis with leave-one-out cross validation. SD = Standard Deviation

* Addition in brackets shows which of the wider regional groupings (*Sus scrofa* only) the sample originates from

E=Europe, NE=Near East, Asia=Mainland Asia, ISEA=Island South East Asia

Groups of differing species are denoted as follows. *S.ahonebarbus* (as is), S.b – *Sus barbatus*, S.ceb – *Sus cebifrons*, S.cel – *Sus celebensis*, S.p – *Sus philippensis*

207 **Methodology**

208 44 homologous, unilateral (right sided), three-dimensional landmarks from the
209 crania of 429 adult (>18 months) *Sus* were digitised using a Microscribetm GLS
210 by J.Owen. Details of the position of the landmarks digitised can be found in the
211 supporting data (table S1). Landmark and observer error was assessed following
212 O'Higgins and Jones (1998) and found to be negligible.

213

214 The base methodology follows standard Geometric Morphometric Methods
215 (GMM) (Zelditch et al., 2004) with landmark co-ordinates superimposed using
216 Generalised Procrustes Analysis (GPA) prior to further analysis. This removes
217 the effect of rotation, scale and location leaving only true shape differences
218 between samples. A measure of size is retained in centroid size, the squared root
219 of the sum of the squared distances between each landmark and the centroid.
220 Centroid size was compared between groups (see table 1) using ANOVA and
221 visualised in a box plot. Overall shape variation was visualized using Principal
222 Components Analysis (PCA). Differences in overall shape between groups were
223 tested using MANOVA and Canonical Variates Analysis (CVA) with
224 permutation tests using Morphoj (Klingenberg, 2008). The morphological
225 differences between group means was described and visualised using a 3D
226 surface scan morphed to different landmark configurations using the EVAN
227 Toolbox (2010). The surface scan was obtained from a wild adult male *S.scrofa*
228 specimen held in the Durham University collections, using a non-contact Konica
229 Minolta Digitiser (v-910).

230

231 Phenotypic relationships were summarised using a dendrogram based on
232 Procrustes distances between group means, and calculated using an unweighted
233 neighbour joining tree (NJ) in NTSys (Rohlf, 2008). The significance of
234 differences between groups was analysed using MANOVA and discriminant
235 function analysis with leave-one-out cross validation in the R statistical
236 environment (See table 2). To analyse wider biogeographic structuring the results
237 of the phenogram were compared with an established genetic phylogeny (Larson
238 et al., 2005) and a traditional biogeographic structure, based on biometric
239 measurements (Groves, 1981, 2007). The phylogeny of Larson et al. (2005) was
240 chosen as it provides the greatest detail of *Sus scrofa*, although several other
241 phylogenies have been published subsequently (Gongora et al., 2011, Mona et
242 al., 2007, Scandura et al., 2011) they concentrate more on family wide overviews
243 (e.g. (Gongora et al., 2011) or on specific regional areas (Scandura et al., 2011)
244 rather than *Sus scrofa* specifically, and do not provide us with a detailed
245 phylogeographic map as Larson et al. (2005) does.

246

247 The relationships between *Sus scrofa* cranial shape and size, and environmental
248 and geographic variables (see table 1), were investigated using multiple linear
249 regression on size (univariate regression) and shape (multivariate regression)
250 following Legendre and Legendre, (1998). Analyses were conducted using the
251 following software packages: Excel (© Microsoft Corporation), Morphologika 2
252 (O'Higgins and Jones, 2006), MorphoJ (Klingenberg, 2008), NTSYS (Rohlf,
253 2008), SPSS 20 (© Microsoft Corporation), R (R Development Core Team,
254 2008), and the EVAN Toolbox, (2010).

255

256 **Results**

257 Significant differences in size were found between geographic groupings of *Sus*
258 *scrofa* ($p < 0.0001$, $F = 7.12$, $df = 25$) and are visually represented in a box plot in
259 figure 2. *S.scrofa* from Europe and the Near East are generally larger than pigs
260 from Asia, and within Europe and the Near East there is a West to East size
261 increase. Pigs from some island samples exhibit the insular dwarfism,
262 specifically the smaller size pigs from Sardinia and Hainan, and in general for
263 *S.scrofa* from ISEA, other *Sus* species in ISEA vary in size from the large *S.*
264 *barbatus* to the small dwarf *S. ahonobarbus*.

265

266 Significant shape differences are evident between groups ($p < 0.0001$ $F = 774.25$,
267 $df = 3125$), although the most pronounced differences exist between *S. scrofa*
268 from Europe and the Near East and *S.scrofa* from Asia (as shown in the CVA in
269 figure 3). PCA of individual specimens shows the overlap and similarity of
270 morphologies in *Sus scrofa*. This is especially true on PC1 (21.18% of total
271 variance), where no discernable geographic discrimination is apparent. On PC2
272 (13.46% of total variance) European and Near Eastern pigs score more highly
273 than pigs from Asia and ISEA, with little overlap between them and the Near
274 Eastern and ISEA pigs. CVA illustrates the differences between groups more
275 clearly. Individuals from Europe and the Near East cluster at the negative end of
276 CV1 (28.272% of variance), individuals from Asia and ISEA at the positive end,
277 with ISEA pigs scoring highest. CV2 (9.487% of variance) splits pigs from the
278 Near East (lower scores) from Europe (higher scores), whilst *S.scrofa* from Asia
279 generally have higher scores on CV2 than *S.scrofa* from ISEA.

280

281 Morphological differences represented by the CVA are visualised in figure 3.
 282 CV1 represents variability around the orbit, with Asian pigs having relatively
 283 larger eyes and more robust zygomatics than European and Near Eastern pigs.
 284 CV2 represents a relative increase in height of the parietal and the nuchal crest,
 285 pigs from Europe and ISEA having higher and wider parietals than pigs from the
 286 Near East or mainland Asia.

287

Original	% Assigned			
	Middle East	Europe	Asia	ISEA
Middle East	79.66	13.56	6.78	0.00
Europe	8.05	89.26	2.01	0.67
Asia	5.41	2.70	82.43	9.46
ISEA	0.00	0.00	7.7	92.30

288 **Table 2:** Results of the discriminant function with leave-one-out cross validation
 289 analysis between the wider regional groupings. Values in bold show the
 290 percentage correctly assigned to group, the non-bold values show where the
 291 misclassified results have been assigned. The table reads left to right for correct
 292 interpretation.

293

294 Discriminant functions with cross validation (Table 2) show the strength of the
 295 morphological identity of the regional groups, both for individual samples and
 296 the four larger regional groupings. The results for individual samples (see
 297 supporting table S2) are, with some exceptions (Sardinia, Japan, Papua and
 298 Geneva), poor, suggesting the morphologies are very similar across species,
 299 which is represented by the results of the individual groups, showing that most of
 300 the incorrect classifications remain within regional groups. The larger regional

301 groupings give far better results; as the CVA plots and the larger clusters on the
302 neighbour joining tree in figure 1 suggest, *Sus scrofa* falls into 4 main bio-
303 geographic groupings supported by high (~80%) or very high (~90%) cross
304 validation scores. Thus between regions there are strongly marked morphological
305 differences but within them it is more difficult to distinguish samples based on
306 morphology alone.

307

308 **Relationships between groups in *Sus scrofa***

309 The neighbour-joining tree in figure 1 shows the morphological relationships
310 within *S.scrofa* in table 1. There are 4 main groups; Europe, the Near East, Asia,
311 and ISEA.

312

313 Starting from the base of the tree the first bifurcation splits pigs from the
314 Caucasus and Berlin from the other pigs. These form a sub-group next to the
315 main European cluster. This cluster contains branches from East Poland and
316 Geneva, then the Island pigs of Sardinia, and finally pigs from South West
317 Poland and South West Germany. This is followed by the Near Eastern group,
318 split into two, first the North African pigs from Tunis and those from Turkey,
319 and then the three Iranian pig groups.

320

321 The next series of bifurcations contains the Asian pigs, first a series of
322 bifurcations splitting the mainland Asian pigs. There is a separate group of the
323 Chinese Island of Hainan and the pigs of Papua, separated from the Asian cluster
324 as they have distinctive cranial morphologies, Hainan as an Island group and
325 Papua as it geographically remote from the other groups. The following

326 bifurcations then split off pigs from South East Asia, Burma, then Malaysia
327 before a final group of pigs from Sumatra.

328

329 **Comparison with previously established biogeographic structure**

330 The map in figure 1 shows the biogeographic distribution of *S.scrofa* according
331 to the phylogeny of Larson et al. (2005). This splits *S.scrofa* (and smaller
332 samples of *Sus celebensis*, *Sus barbatus* and *Sus verrucosus*) into 14 haplotypes.
333 Two represent suids from Sulawesi and one included *S.scrofa* and *S.barbatus* and
334 *S.verrucosus*, the remainder represent various geographic groupings of *S.scrofa*.
335 Europe contains two haplotypes, one found only in Italy and Sardinia, and the
336 other in the rest of Europe. The Near East contains a separate haplotype and the
337 remainder are found in Asia, with several on the mainland and the others in
338 ISEA. This phylogeographic ordering broadly corresponds to the traditional
339 morphometric assignment of 4 main groups; the ‘Western’ group of Europe,
340 North Africa and the Middle East; the ‘Indian’ group from Eastern Iran to
341 Thailand; the ‘Eastern’ group from Mongolia and Russia to China and Vietnam;
342 and the ‘Indonesian’ group from the Malay peninsula through the Indonesian
343 islands (Groves, 2007).

344

345 Our results mirror those generated from genetic data more closely than those
346 from traditional morphological studies. The tree in figure 1 shows European,
347 Near Eastern, Mainland Asian and ISEA groupings. It splits the Western race
348 into Europe and the Near East (with the small African sample falling in the Near
349 Eastern group); the Indian and Eastern races are merged, although there are few
350 Indian samples so this result must be treated with caution. The Indonesian race of

351 ISEA is supported as a separate entity, as it is both the genetic and traditional
352 morphometric studies.

353

354 **The effect of climate and geography on *Sus* cranial shape and size**

355 Multiple linear regression of size against the geographic and environmental co-
356 variates show that size is positively correlated with them ($r=0.652$, $r^2=0.425$,
357 adjusted $r^2=0.248$, $F=2.398$, $p=0.044$). Examination of the significant individual
358 predictors against size show that longitude ($r=-0.49$, $p<0.001$), temperature ($r=-$
359 0.426 , $p=0.005$), rainfall ($r=-0.566$, $p<0.001$) and the SD of rainfall ($r=0.341$,
360 $p=0.023$) are negatively correlated; while latitude ($r=0.547$, $p<0.001$) and the SD
361 of temperature ($r=0.559$, $p<0.001$) are positively correlated. Neither elevation
362 ($R=0.148$, $p=0.198$) or the Shannon index ($r=-0.179$, $p=0.152$) were significant.

363

364 Multiple multivariate linear regression of shape against the geographic and
365 environmental co-variates show that longitude ($r^2=0.972$, $F=24.258$, $p<0.001$),
366 latitude ($r^2=0.972$, $F=10.51$, $p<0.001$), temperature ($r^2=0.816$, $F=3.113$,
367 $p=0.017$), SD of temperature ($r^2=0.906$, $F=6.723$, $p<0.001$) and rainfall
368 ($r^2=0.925$, $F=8.606$, $p<0.001$) are significant predictors. Elevation ($r^2=0.642$,
369 $F=1.257$, $p=0.335$), SD of monthly rainfall ($r^2=0.479$, $F=0.643$, $p=0.821$) or the
370 Shannon index ($r^2=0.731$, $F=1.905$, $p=0.11$) were significant.

371

372 Neither the Shannon index or elevation are significantly correlated to size or
373 shape, while the SD of monthly rainfall correlates with size but not shape.
374 Latitude, longitude, temperature, the SD of temperature and rainfall all have an
375 effect on size and shape of the suid skull.

376 **Discussion**

377 **Biogeography**

378 *Sus scrofa* shows clear biogeographic ordering, with regional groupings of
379 Europe, the Near East, Asia and ISEA. The GM results give a clearer resolution
380 than do traditional biometrics, splitting the European and Near Eastern *S.scrofa*
381 groups apart, concurrent with the genetics, where as the traditional biometrics
382 conflates them.

383

384 The GM results split the Papua group from the rest of the ISEA samples,
385 following Larson et al. (2005); the *Sus* from eastern ISEA are different from *Sus*
386 from Malaysia and Sumatra. The Sardinian group in the European cluster are
387 separate, in concordance with genetic evidence that they are a separate haplotype
388 and perhaps even a separate subspecies (*S.scrofa meridionalis* (Groves, 1981).
389 Japanese pigs are separated by morphology using both GM and traditional
390 biometrics (as *S.scrofa leucomystax*) but not by genetics where they form part of
391 the mainland Asia clade, thus the morphology maybe reflecting some form of
392 insularity. One problem with the GM results is that they amalgamate the
393 mainland Asia pigs into a single unit whereas the genetic results show that there
394 are several haplotypes present, and the traditional biometrics suggest two
395 groupings (Eastern and Indian races). This is likely due to a paucity of data from
396 this region and future analysis may grant better resolution.

397

398 **Effects of climate and geography on shape and size**

399 Both skull size and shape in wild *Sus scrofa* is highly variable across Eurasia,
400 showing significant correlation to longitude, latitude, temperature and rainfall
401 variables for both size and shape.

402

403 That geography contributes to shape variation is of particular interest as it affirms
404 what several genetic studies have suggested, that at localised levels wild boar are
405 split into different populations (Ferreira et al., 2009, Nikolov et al., 2009),
406 although topological features could not completely explain their presence
407 (Scandura et al., 2011).

408

409 Mean annual precipitation was a significant predictor of shape and its standard
410 deviation a significant predictor of shape and size. That annual precipitation (and
411 SD of annual precipitation) suggests that shape and size change in *Sus* in Europe
412 and the Near East are effected by diet and habitat as well as thermo regulation
413 and Bergman's rule, precipitation being used here as a rough proxy for habitat
414 productivity influencing size by food availability (Cardini et al., 2007).

415

416 There is also a strong longitudinal west – east size increase across Europe present
417 in our data (see box plot in figure 2) which has been noted before in both *Sus*
418 *scrofa* (Albarella et al., 2009, Genov, 1999) and reindeer (Weinstock, 2000) and
419 is linked to the harsh winters of Eastern Europe bottlenecking the population,
420 reducing population density and competition for resources allowing individuals
421 to grow larger (Weinstock, 2000). As such European *S.scrofa* does not conform
422 to Bergman's rule which links size to latitudinal gradients (contra (Davis, 1981),

423 confirming that factors other than temperature are significant in size and shape
424 variability.

425

426 *Sus scrofa* responds to insularity though dwarfism. Pigs from Sardinia and
427 Hainan are smaller than pigs from the nearby mainland, and pigs from ISEA are
428 in general smaller than those from mainland Asia. The exception to this are pigs
429 from Japan, which show no sign of size reduction, possibly as Japan is an island
430 large enough not to trigger a dwarfing effect.

431

432 **Conclusion**

433 *Sus scrofa* is a species that shows strong biogeographic structuring, reflecting its
434 large range throughout Eurasia and North Africa (Gongora et al., 2011, Lucchini
435 et al., 2005, Scandura et al., 2011). This can be traced through both its genetics
436 and morphology; although using a GMM approach on cranial morphology gives
437 greater depth of resolution than do traditional biometrics, confirming that this
438 approach has great scope for use in biogeographic studies (Cardini et al., 2007,
439 Cardini and Elton, 2009). This is important where subspecies have been ascribed
440 largely on the basis of cranial characteristics (Groves, 1981, 2007, Genov, 1999),
441 which often rely on order of magnitude measurements (and are thus more limited
442 in the amount of shape variation they contain); it is possible that they may need
443 re-assessing in the light of recent phylogenetic and morphometric
444 methodological advances.

445

446 These results are also significant with regard to studies of determination of status
447 as wild or domestic, these too are mainly based on size differences (Payne and

448 Bull, 1988, Mayer et al., 1998). These investigations are based on the assumption
449 that wild and domestic individuals are morphologically different from each other
450 and that this difference is significant, be it in cranial characteristics, tooth size or
451 overall body size. However, these characteristics are strongly affected by
452 climate, diet, habitat and geography, making the individuals a product of their
453 surroundings. Studies investigating domestic status of suids must therefore take
454 into account possible dietary changes or environmental shifts. This will mainly
455 affect regional or wide temporal studies which should include baseline
456 comparisons with wild animals and other domestics to check for possible
457 climatic shifts.

458

459 **Acknowledgements**

460 This project was supported by NERC (NE/F003382/1) and The Leverhulme
461 Trust (F/00 128/AX). We thank Frieder Mayer and Saskia Janke at the Museum
462 für Naturkunde Berlin; Richard Sabin at the London Natural History Museum;
463 Cécile Callou and Joséphine Lesur at Muséum National d'Histoire Naturelle,
464 Paris; Jacqueline Studer and Manuel Ruedi at Muséum d'histoire naturelle de la
465 Ville de Genève; Renate Schafberg at der Museum fur Haustierkunde, Halle;
466 William Stanley of the Field Museum of Natural History; Eileen Westwig at the
467 American Museum of Natural History; Melinda Zeder at the Smithsonian MSC,
468 Washington DC and Alastair Macdonald at the Royal (Dick) School of
469 Veterinary Studies for access to collections and for all their help. We also thank
470 Thomas Cucchi, Arden Hulme-Beamen and Linus Girdland-Flink for their
471 contributions to data collection and comments on drafts of this paper.

472

473

474 **Bibliography**

- 475 ALBARELLA, U., DOBNEY, K., ERVYNCK, A. & ROWLEY-CONWY, P.
 476 2007. Introduction. In: ALBARELLA, U., DOBNEY, K., ERVYNCK,
 477 A. & ROWLEY-CONWY, P. (eds.) *Pigs and Humans: 10,000 Years of*
 478 *Interaction*. Oxford: Oxford University Press.
- 479 ALBARELLA, U., DOBNEY, K. & ROWLEY-CONWY, P. 2009. Size and
 480 shape of the Eurasian wild boar (*Sus scrofa*), with a view to the
 481 reconstruction of its Holocene history. *Environmental Archaeology*, 14,
 482 103-136.
- 483 ALVES, P. C., PINHEIRO, I., GODINHO, R., VICENTE, J., GORTAZAR, C.
 484 & SCANDURA, M. 2010. Genetic diversity of wild boar populations and
 485 domestic pig breeds (*Sus scrofa*) in South-western Europe. *Biological*
 486 *Journal of the Linnean Society*, 101, 797-822.
- 487 BIRKHOFER, K. & WOLTERS, V. 2012. The global relationship between
 488 climate, net primary production and the diet of spiders. *Global Ecology*
 489 *and Biogeography*, 21, 100-108.
- 490 BRONIKOWSKI, A. & WEBB, C. 1996. Appendix: A critical examination of
 491 rainfall variability measures used in behavioral ecology studies.
 492 *Behavioral Ecology and Sociobiology*, 39, 27-30.
- 493 CARDINI, A. & ELTON, S. 2009. Geographical and taxonomic influences on
 494 cranial variation in red colobus monkeys (Primates, Colobinae):
 495 introducing a new approach to 'morph' monkeys. *Global Ecology and*
 496 *Biogeography*, 18, 248-263.
- 497 CARDINI, A., JANSSON, A. U. & ELTON, S. 2007. A geometric
 498 morphometric approach to the study of ecogeographical and clinal
 499 variation in vervet monkeys. *Journal of Biogeography*, 34, 1663-1678.
- 500 DAVIS, S. J. M. 1981. The Effects of Temperature Change and Domestication
 501 on the Body Size of Late Pleistocene to Holocene Mammals of Israel.
 502 *Paleobiology*, 7, 101-114.
- 503 DINU, A. 2009. The action of the masticatory muscles and cranial changes in
 504 pigs as results of domestication. *Documenta Praehistorica*, 36, 207-218.
- 505 ENDO, H., HAYASHI, Y., YAMAZAKI, K., MOTOKAWA, M., PEI, J.-C. K.,
 506 LIN, L.-K., CHOU, C.-H. & OSHIDA, T. 2002. Geographical Variation
 507 of Mandible Size and Shape in the Wild Pig (*Sus scrofa*) from Taiwan
 508 and Japan. *Zoological Studies*, 41, 452-460.
- 509 EVAN TOOLBOX. 2010. <http://evan-society.org/node/42> [Online].
- 510 FERREIRA, E., SOUTO, L., SOARES, A. M. V. M. & FONSECA, C. 2009.
 511 Genetic structure of the wild boar population in Portugal: Evidence of a
 512 recent bottleneck. *Mammalian Biology*, 74, 274-285.
- 513 FULLER, M. F. 1965. EFFECT OF ENVIRONMENTAL TEMPERATURE ON
 514 NITROGEN METABOLISM AND GROWTH OF YOUNG PIG. *British*
 515 *Journal of Nutrition*, 19, 531-&.
- 516 GENOV, P. V. 1999. A Review of the Cranial Characteristics of the Wild Boar
 517 (*Sus scrofa* Linnaeus 1758), with Systematic Conclusions. *Mammal*
 518 *Review*, 29, 205-238.
- 519 GONGORA, J., CUDDAHEE, R. E., NASCIMENTO, F. F. D., PALGRAVE, C.
 520 J., LOWDEN, S., HO, S. Y. W., SIMOND, D., DAMAYANTI, C. S.,
 521 WHITE, D. J., TAY, W. T., RANDI, E., KLINGEL, H., RODRIGUES-
 522 ZARATE, C. J., ALLEN, K., MORAN, C. & LARSON, G. 2011.

- 523 Rethinking the evolution of extant sub-Saharan African suids (Suidae,
524 Artiodactyla). *Zoologica Scripta*, 40, 327-335.
- 525 GROVES, C. 1981. *Ancestors for the Pigs: Taxonomy and Phylogeny of the*
526 *Genus Sus*, Canberra, Research School of Pacific Studies, Australian
527 National University.
- 528 GROVES, C. 2007. Current views on taxonomy and zoogeography of the genus
529 *Sus*. In: ALBARELLA, U., DOBNEY, K. & ROWLEY-CONWY, P.
530 (eds.) *Pigs and Humans: 10,000 years of interaction*. Oxford: Oxford
531 University Press.
- 532 GRUBB, P. 1993. *Eurasian Suids Sus and Babyrousa.*, Cornell University,
533 IUCN.
- 534 HADLEY, C., MILNE, N. & SCHMITT, L. 2009. Geographical and historical
535 influences on cranial size and shape in tammar wallaby (*Macropus*
536 *eugenii*) populations. *Homo-Journal of Comparative Human Biology*, 60,
537 271-271.
- 538 HAFEZ, E. S. E. 1968. *Adaption of Domestic Animals*, Philadelphia, Lea &
539 Febiger.
- 540 HERRING, S. W., RAFFERTY, K. L., LIU, Z. J. & MARSHALL, C. D. 2001.
541 Jaw muscles and the skull in mammals: the biomechanics of mastication.
542 *Comparative Biochemistry and Physiology a-Molecular & Integrative*
543 *Physiology*, 131, 207-219.
- 544 KLINGENBERG, C. P. 2008. *Morphoj* [Online]. University of Manchester, UK.:
545 Faculty of Life Sciences. Available:
546 http://www.flywings.org.uk/MorphoJ_page.htm.
- 547 LARSON, G., DOBNEY, K., ALBARELLA, U., FANG, M. Y., MATISOO-
548 SMITH, E., ROBINS, J., LOWDEN, S., FINLAYSON, H., BRAND, T.,
549 WILLERSLEV, E., ROWLEY-CONWY, P., ANDERSSON, L. &
550 COOPER, A. 2005. Worldwide phylogeography of wild boar reveals
551 multiple centers of pig domestication. *Science*, 307, 1618-1621.
- 552 LARSSON, E., OGAARD, B., LINDSTEN, R., HOLMGREN, N.,
553 BRATTBERG, M. & BRATTBERG, L. 2005. Craniofacial and
554 dentofacial development in pigs fed soft and hard diets. *American*
555 *Journal of Orthodontics and Dentofacial Orthopedics*, 128, 731-739.
- 556 LEGENDRE, P. & LEGENDRE, L. 1998. *Numerical Ecology: Second English*
557 *Edition*, Oxford, Elsevier.
- 558 LUCCHINI, V., MEIJAARD, E., DIONG, C. H., GROVES, C. P. & RANDI, E.
559 2005. New phylogenetic perspectives among species of South-east Asian
560 wild pig (*Sus* sp.) based on mtDNA sequences and morphometric data.
561 *Journal of Zoology*, 266, 25-35.
- 562 MASSEI, G. & GENOV, P. V. 2004. The Environmental Impact of Wild Boar.
563 *Galemys*, 16, 135-145.
- 564 MAYER, J. J., NOVAK, J. M. & BRISBIN JR., I. L. 1998. Evaluation of Molar
565 Size as a Basis for distingusiing Wild Boar from Domestic Swine:
566 Employing the Present to Decipher the Past. In: NELSON, S. M. (ed.)
567 *Ancestors for the Pigs: Pigs in Prehistory*. Philadelphia: Museum
568 Applied Science Centre for Archaeology.
- 569 MAYR, E. 1954. Geographical character gradients and climatic adaptation.
570 *Evolution*, 10, 105-108.
- 571 MEIRI, S. 2008. Evolution and ecology of lizard body sizes. *Global Ecology and*
572 *Biogeography*, 17, 724-734.

- 573 MEIRI, S. & DAYAN, T. 2003. On the validity of Bergmann's rule. *Journal of*
574 *Biogeography*, 30, 331-351.
- 575 MEIRI, S., DAYAN, T. & SIMBERLOFF, D. 2005. Variability and sexual size
576 dimorphism in carnivores: Testing the niche variation hypothesis.
577 *Ecology*, 86, 1432-1440.
- 578 MEIRI, S., DAYAN, T. & SIMBERLOFF, D. 2006. The generality of the island
579 rule reexamined. *Journal of Biogeography*, 33, 1571-1577.
- 580 MEIRI, S., RAIA, P. & PHILLIMORE, A. B. 2011. Slaying dragons: limited
581 evidence for unusual body size evolution on islands. *Journal of*
582 *Biogeography*, 38, 89-100.
- 583 MILLIEN, V., KATHLEEN LYONS, S., OLSON, L., SMITH, F. A., WILSON,
584 A. B. & YOM-TOV, Y. 2006. Ecotypic variation in the context of global
585 climate change: revisiting the rules. *Ecology Letters*, 9, 853-869.
- 586 MONA, S., RANDI, E. & TOMMASEO-PONZETTA, M. 2007. Evolutionary
587 history of the genus *Sus* inferred from cytochrome b sequences.
588 *Molecular Phylogenetics and Evolution*, 45, 757-762.
- 589 MURRAY, A. 1978. *The geographical distribution of mammals*, New York,
590 Arno press.
- 591 NIKOLOV, I. S., GUM, B., MARKOV, G. & KUEHN, R. 2009. Population
592 genetic structure of wild boar *Sus scrofa* in Bulgaria as revealed by
593 microsatellite analysis. *Acta Theriologica*, 54, 193-205.
- 594 O'HIGGINS, P. & JONES, N. 1998. Facial growth in *Cercocebus torquatus*: an
595 application of three-dimensional geometric morphometric techniques to
596 the study of morphological variation. *Journal of Anatomy*, 193, 251-272.
- 597 O'HIGGINS, P. & JONES, N. 2006. *Tools for statistical shape analysis* [Online].
598 Hull York Medical School. Available:
599 <http://sites.google.com/site/hymsfme/resources>.
- 600 OLIVER, W. 1993. *Pigs, Peccaries and Hippos*, Gland Switzerland, IUCN.
- 601 OLIVER, W. 2010. *Sus ahoenobarbus*: IUCN Red List of Threatened Species
602 [Online]. Available: www.iucnredlist.org.
- 603 OLIVER, W. & LEUS, K. 2008. *Sus scrofa* [Online]. IUCN. Available:
604 www.iucnredlist.org [Accessed 2/21/2012 2012].
- 605 PAYNE, S. & BULL, G. 1988. Components of variation in measurements of pig
606 bones and teeth, and the use of measurements to distinguish wild from
607 domestic pig remains. *Archaeozoologia*, 2, 27-65.
- 608 R DEVELOPMENT CORE TEAM 2008. *R: A language and environment for*
609 *statistical computing*, Vienna, Austria, R Foundation for Statistical
610 Computing.
- 611 ROHLF, F. J. 2008. *NTSYSpc: Numerical Taxonomy System* [Online]. Setauket,
612 NY: Exeter Publishing, Ltd.
- 613 ROWLEY-CONWY, P., ALBARELLA, U. & DOBNEY, K. 2012.
614 Distinguishing Wild Boar from Domestic Pigs in Prehistory: A Review of
615 Approaches and Recent Results. *Journal of World Prehistory*, 25, 1-44.
- 616 SACK, W. O. 1982. *Essentials of Pig Anatomy: Horowitz/Kramer Atlas of*
617 *Musculoskeletal Anatomy of the Pig*, Ithaca, New York, Veterinary
618 Textbooks.
- 619 SCANDURA, M., IACOLINA, L. & APOLLONIO, M. 2011. Genetic diversity
620 in the European wild boar *Sus scrofa*: phylogeography, population
621 structure and wild x domestic hybridization. *Mammal Review*, 41, 125-
622 137.

- SCHOLANDER, P. F. 1955. Evolution of climatic adaptation in homeotherms. *Evolution*, 9, 15-26.
- SCHOLANDER, P. F. 1956. Climatic rules. *Evolution*, 10, 39-40.
- UZAL, A. & NORES, C. 2004. Endogenous and Exogenous constraints in the population changes of Wild Boar (*Sus scrofa* Linnaeus, 1758). *Galemys*, 16, 83-98.
- VAN CAKENBERGHE, V., HERRAL, A. & AGUIRRE, L. F. 2002. Evolutionary Relationships between Cranial Shape and Diet in Bats (Mammalia: Chiroptera). In: AERTS, P., D'AOÛT, K., HERRAL, A. & VAN DAMME, R. (eds.) *Topics in Functional and Ecological Vertebrate Morphology*. Shaker Publishing.
- VIGUIER, B. N. 2002. Is the morphological disparity of lemur skulls (Primates) controlled by phylogeny and/or environmental constraints? *Biological Journal of the Linnean Society*, 76, 577-590.
- WEINSTOCK, J. 2000. *Late Pleistocene reindeer populations in Middle and Western Europe. An Osteometrical Study of Rangifer Tarandus*, Tübingen, Mo Vince Verlag.
- WOLFF, J. 1986. *The Law of Bone Remodeling (translation of the German 1892 edition)*, New York, Springer.
- YOM-TOV, Y. & GEFFEN, E. 2006. Geographic variation in body size: the effects of ambient temperature and precipitation. *Oecologia*, 148, 213-218.
- ZELDITCH, M. L., DONALD, L., SWIDERSKI, H., SHEETS, D. & FINK, W. L. 2004. *Geometric Morphometrics for Biologists: A Primer*, London, Elsevier Academic Press.

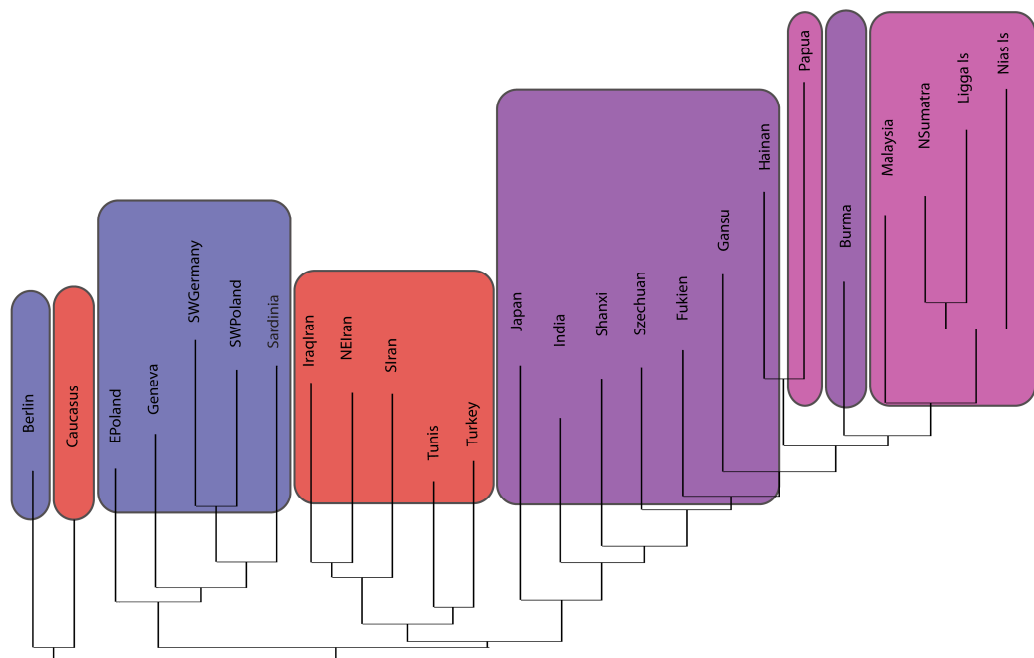
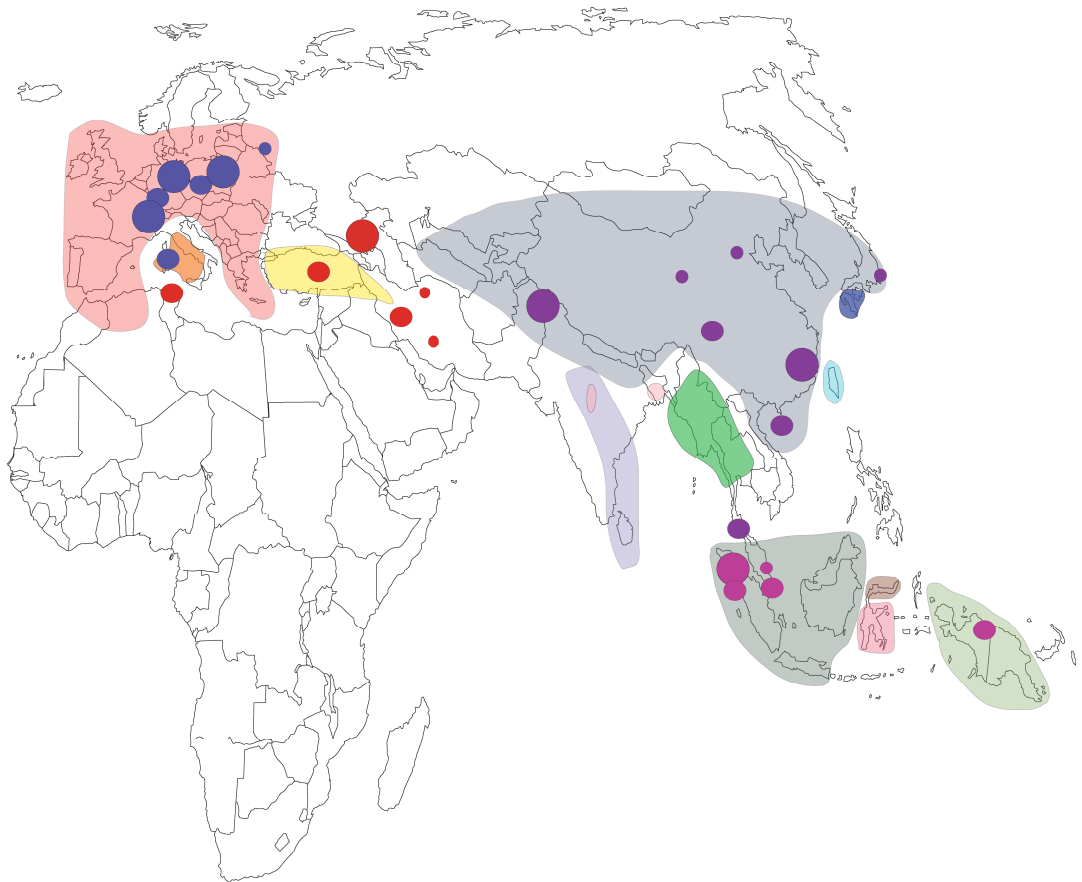
Figure 1: Map of samples overlaid on a map of mtDNA groups from Larson et al. (2005), with accompanying Neighbour Joining tree showing the phenetic relationships between samples. Dots represent samples from this study, shaded areas follow Larson et al. Blue = European *S.scrofa*, Red = Near Eastern, Dark Purple Asian, Light Purple = ISEA.

Figure 2: Box plot of centroid sizes, colours follow that of figure 1.

Figure 3: PCA (top) and CVA (bottom) of *Sus scrofa* samples, colours follow that of figure 1.

658 **Figure 1**

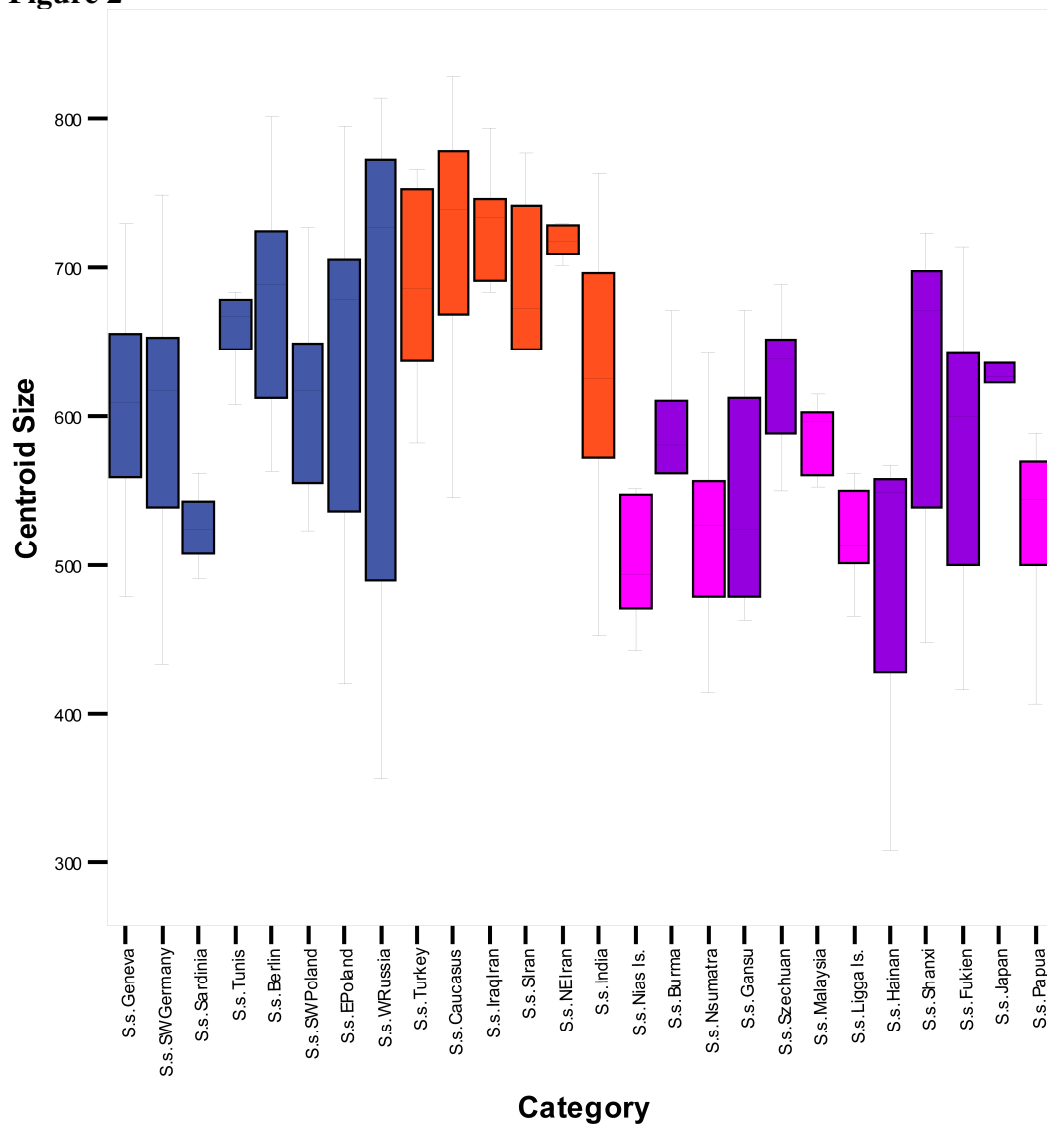
659



660

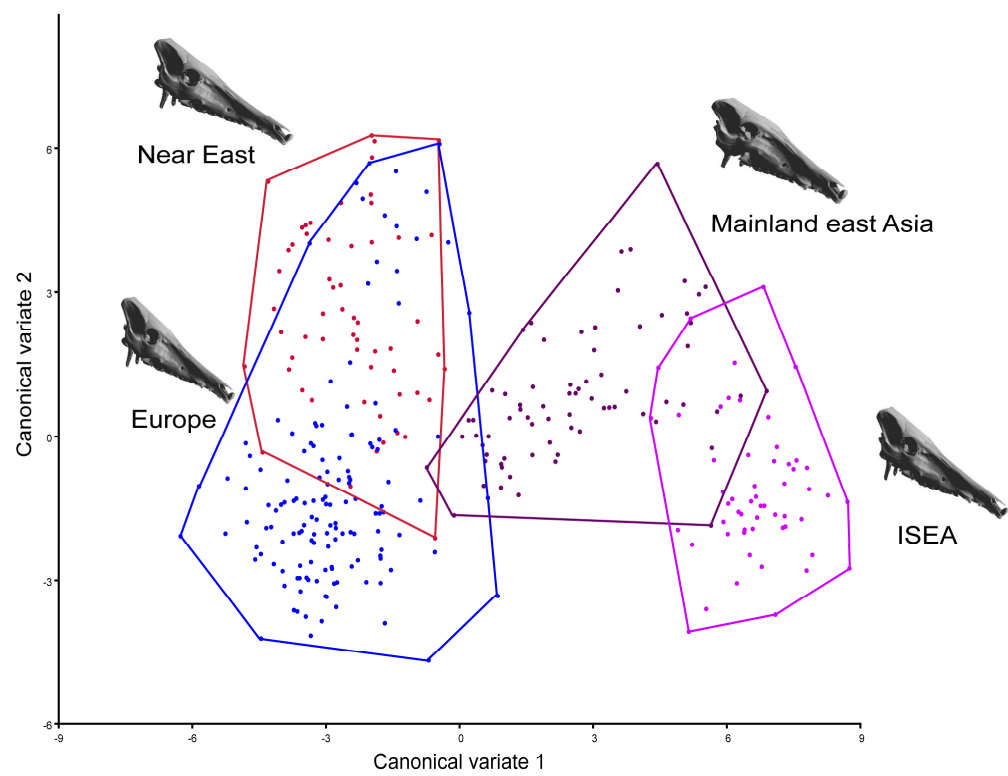
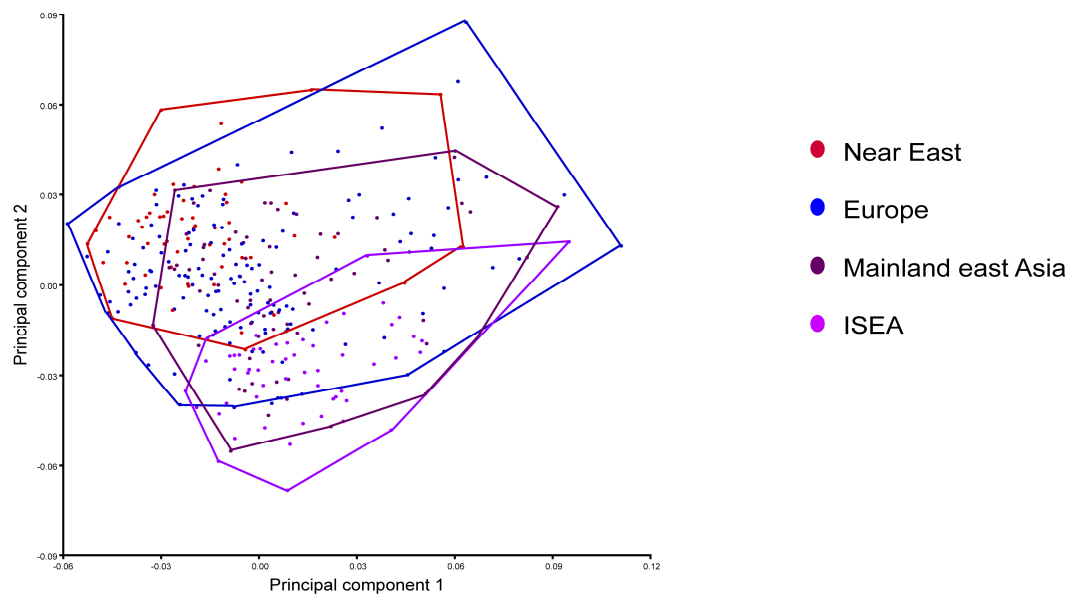
661

662 **Figure 2**



663
664

665 **Figure 3**
 666



667
 668

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18

Chapter 5

Manuscript 3

Quantifying cranial shape differences between wild boar and domestic pigs (*Sus scrofa*) using 3D geometric morphometrics and its application to zooarchaeology

Quantifying cranial shape differences between wild boar and domestic pigs (*Sus scrofa*) using 3D geometric morphometrics and its application to zooarchaeology

Joseph OWEN^{a,b}, Keith DOBNEY^c, Allowen EVIN^{c,d} Thomas CUCCHI^{c,d}, Peter ROWLEY-CONWY^a, Greger LARSON^a and Una STRAND VIDARSDOTTIR^b.

^aDepartment of Archaeology, University of Durham, South Road, Durham DH1 3LE, United Kingdom. J.t.d.owen@durham.ac.uk; p.a.rowley-conwy@durham.ac.uk; greger.larson@durham.ac.uk.

^dDepartment of Anthropology, University of Durham, South Road, Durham DH1 3LE, United Kingdom. una.vidarsdottir@durham.ac.uk

^cDepartment of Archaeology, University of Aberdeen, St.Mary's Building, Elphinstone Road, United Kingdom. a.evin@abdn.ac.uk; keith.dobney@abdn.ac.uk.

^dCNRS-Muséum National d'Histoire Naturelle, UMR 7209, Archéozoologie, histoire des sociétés humaines et de peuplements animaux, 55 rue Buffon, 75005 Paris, France. evin@mnhn.fr; cucchi@mnhn.fr.

Abstract

The process of domestication increases the variety of phenotypes expressed in animals. Zooarchaeologists have attempted to study these changes osteologically in their search for the geographic origins and temporal context of the initial animal domestication during the early Holocene. Traditional biometrical approaches have explored changes in body size over time, but given poor resolution and been adversely affected by confounding factors such as climate, sex, diet and disease. Here we investigate whether geometric morphometric analyses of cranial shape can be used to provide better resolution between wild and domestic pigs (*Sus scrofa*), as we know that shape is less affected by epigenetic factors than is size. Geometric morphometric methods with traditional multivariate statistics were applied to 52 modern domestic (6 breeds) and 142 wild adult pig crania. Further analyses were carried out on morphologically discrete portions of the whole skull to simulate the fragmented nature of archaeological mammal remains. Highly significant discrimination was found between wild and domestic pigs from analyses of the whole skull, the parietal, the basicranium, the angle of the nasal and the zygomatic. It is also possible to discriminate between crania from different domestic breeds. Our

53 data shows that geometric morphometric techniques could successfully be applied in
54 zooarchaeology to provide a much better, quantifiable resolution between wild and
55 domestic pigs, even on the basis of partial cranial remains.

56

57 **Introduction**

58 The domestication of plants and animals was a key part of the transition of human
59 subsistence strategies from hunter-gatherers to sedentary farmers, during the early
60 Neolithic. Studies of this transition include those locating and analysing the origins
61 and methodologies of animal domestication (Rowley-Conwy et al., 2012), which
62 require the ability to distinguish between wild and domestic animals.

63

64 The morphological determination of wild and domestic animals relies upon the
65 presence of derived or altered characters in the domestic forms compared to their
66 wild ancestor. The traditional methodology of wild-domestic assignation in the
67 archaeozoological record is largely based on size reduction of either teeth (Mayer et
68 al., 1998) or bone (Albarella, 2002, Ervynck et al., 2001, Payne and Bull, 1988, von
69 den Driesch, 1976) in early domesticated animals. Yet there is a major issue with this
70 methodology in that size is affected by both genetic and epigenetic factors (Vigne et
71 al., 2005) such as temperature, climate, diet, sexual dimorphism and individual
72 variation. Climatic and environmental conditions, specifically precipitation, have a
73 significant impact on body size, as moisture is linked to primary productivity and
74 food availability (Cardini and Elton, 2009, Meiri and Dayan, 2003). Comparative
75 morphology can still be informative on the wild or domestic status of animals in the
76 past if the issues associated with size are rectified e.g. climatic variation can be
77 overcome by comparing samples from similar habitats and with adequate temporal
78 sequences (to eliminate the affect of climate change over time). Such corrections are
79 subject to the availability of well dated large samples and relevant climatic data, and
80 this often excludes inter-regional comparisons (Rowley-Conwy et al., 2012).
81 Alternatively, methodologies that study shape instead of size, like geometric
82 morphometrics (GM) can provide an approach that is less affected by these biases
83 (Vigne et al., 2005). Shape is determined more by genetically inherited traits and less
84 by environment or diet, and is thus more informative than size if studied in a
85 multivariate statistical environment (Zelditch et al., 2004).

86

87 The morphological changes caused by domestication have been well documented
88 (Clutton-Brock, 1988). In his two part volume dedicated to the evolution of domestic
89 species and the differences between them and their wild progenitors Darwin was the
90 first to note that virtually all domesticated animals had undergone similar phenotypic
91 and physiological changes (Darwin, 1868). These changes include the appearance of
92 dwarf or giant varieties, piebald colouring, curly hair, shortened or rolled tails,
93 floppy ears and changes in the reproductive cycle of most domesticated species
94 (Trut, 1999). It also includes ‘paedomorphic’ changes to the crania, expressed as
95 snout shortening and increased concavity of the face, braincase reduction, tooth
96 crowding and tooth length reduction, which in turn is linked to body size reduction in
97 many species, including pigs and dogs (Cucchi et al., 2011).

98
99 The causal mechanisms of morphological change during domestication are, poorly
100 understood. Some of these modifications may result from hormonal changes due to
101 environmental conditions and the stress of captivity, i.e. without human intent
102 (Arbuckle, 2005, Künzl et al., 2003). Others may stem from
103 epigenetic/developmental changes, or as expressions of genetic mutations directly
104 selected for by humans (Price, 1984, Price, 1999, Vigne, 2011). Experimental data
105 suggest that morphological changes may be triggered by selection along developmental
106 pathways that control the physiological systems responsible for reduced
107 aggressiveness (Arbuckle, 2005, Trut, 1999, Zeder, 2012). This has been
108 demonstrated in a breeding experiment of silver foxes (*Vulpes vulpes*) (Belyaev,
109 1969, Belyaev, 1979), where selection was based on a single criterion – reduced
110 aggression towards human handlers (Trut, 1999). This experiment produced an entire
111 suite of phenotypic changes found in domestic animals within as few as 8 to 10
112 generations (Trut, 1999). Rapid development of the domestic phenotype has been
113 explained by a hypothesis of heterochrony - alterations in the rate of development
114 (Gould, 1977, Hare et al., 2012), and suggestions that domestication may have
115 accelerated the attainment of sexual maturity (Price, 1999). However, the traditional
116 methodology used to test for heterochrony has recently been challenged
117 (Mitteroecker et al., 2005) and the theory that dogs (*Canis lupus*) are paedomorphic
118 wolves rejected (Drake, 2011). Despite the uncertainty about the root causes of
119 morphological change in domestic animals the point stands that wild and domestic
120 animals may be distinguished by their morphology.

121

122 To quantify the differences between wild and domestic cranial morphologies we
123 applied a three dimensional Geometric Morphometrics (GMM) approach to pig
124 crania. Pigs were chosen for this study as they have been an important resource
125 throughout human history and are one of the first major livestock domesticates
126 (Vigne, 2011). The evolution of pig morphology and behaviour in response to
127 domestication, and the co-adaptation of pigs and humans, has been intensively
128 studied over the last decades (Clutton-Brock, 1988, Price, 1984, Rosenberg and
129 Redding, 1998, Scandura et al., 2011, Vigne, 2011, Zeder, 2006, 2012, Zeuner,
130 1963). They were and remain a major global food source and of central importance
131 to the development of human societies across the world. We focus on crania as they
132 have a noted response to domestication (Darwin, 1868) and can be used as a proxy
133 for the post-cranial skeleton (Cardini et al., 2007). In order to determine whether, and
134 how accurately, cranial morphology can be used to distinguish between wild-
135 domestic pigs we apply GMM and traditional multivariate statistics to a single, well
136 defined wild population and several different domestic breeds. To replicate the
137 affects of the taphonomic processes bones may be subjected to in the archaeological
138 record, e.g. breaking or abrasion (Lyman, 1994), we analyse specific regions of the
139 skull, again quantifying differences in morphology and testing their accuracy.

140

141 The study of animal ‘improvement’ (selective breeding to promote desired traits) and
142 the origin of breeds is an important one, as there is a suggestion that this practice
143 occurred before the agricultural revolution of the 18th century (Davis et al., 2012) and
144 the origin of many domestic breeds is unknown. Like the study of domestication,
145 evidence for improvement is based on size increases over time, interpreted as
146 deliberate breeding for larger animals (Davis, 2008), but with the same problems as
147 using size to determine wild-domestic status. To determine whether it is possible to
148 discriminate between domestic breeds on the basis of cranial morphology, we apply
149 GMM to a variety of domestic pig breeds.

150

151 **Materials**

152 Our sample comprised 52 domestic and 142 wild adult (>18 months) *S. scrofa*
153 crania. The domestic pigs were recorded in the “Julius Kühn” Museum für
154 Haustierrkunde in Halle, East Germany where they were born, bred and slaughtered.

155 The wild pigs are housed in the Natural History Museum in Berlin and originate
156 from the Białowiecki national park in East Poland, and the vicinity of Nysa, South-
157 West Poland. We chose a wild population from a limited region to reduce the
158 confounding effects of geographic and climatic induced morphological variation that
159 exists in *Sus*. The domestic breeds were Berkshire, Cornwall, Tamworth, Veredeltes
160 Landschwein, Hannover-Braunschweig Landschwein and Deutsches Edelschwein, as
161 well as a small sample of first generation Tamworth-Wild pig hybrids (domestic
162 sows and wild boars). See supporting table (S1) for further details.

163

164 **Methods**

165 Forty-four unilateral three-dimensional coordinates were digitised from the right side
166 of the cranium, using a Microscribe® GLS (EMicroscribe Inc), by the first author,
167 and analysed using Geometric morphometric methods (GMM (Bookstein, 1991,
168 O'Higgins, 2000, Mitteroecker and Gunz, 2009). Specimens were standardised
169 (scaled, transposed and rotated) using a Generalised Procrustes Analysis (GPA)
170 superimposition (Rohlf, 2003, Zelditch et al., 2004). GPA removes size but allows
171 reintroduction into the analysis when relevant as Centroid Size (CS). CS is a
172 geometric scale defined as the square root of the sum of squared distances between
173 all landmarks and their centroid. Differences in size between groups were assessed
174 with one-way ANOVA and explored with multivariate regression on pooled within
175 group variation of both wild and domestic samples.

176

177 Principal Component Analysis (PCA) was used for initial data exploration and
178 dimensionality reduction of morphological relationships between different groups.
179 The morphological differences between group means were described and visualised
180 using a 3D surface scan morphed to different landmark configurations using the
181 EVAN Toolbox (2010). The surface scan was taken from a wild adult male *S.scrofa*
182 specimen held in the Durham University collections, using a non-contact Konica
183 Minolta Digitiser (v-910). Significance of differences in shape between groups (wild
184 vs. domestic and between domestic breeds) was assessed using Multivariate Analysis
185 of Variance (MANOVA). To assess the significance of differences between group
186 shapes, discriminant functions with leave-one-out cross-validation were applied to
187 the principle component scores. This was conducted on a reduced set of principal
188 components to avoid over fitting the data (Kovarovic et al., 2011). Analysis was

189 conducted in MorphoJ (Klingenberg, 2008) and in the R statistical environment
190 (version 2.13.0 R Development Core Team).

191

192 The dataset was broken down into smaller subsets of landmarks (see supplementary
193 table S2), chosen to represent specific regions of the skull: the parietal, the
194 zygomatic, the angle of the nasal, the orbit, the tooth row and the basicranium to
195 determine areas of maximum discrimination which can then be applied to
196 fragmentary archaeological material. The regions were chosen on their likely ability
197 to distinguish between wild and domestic *Sus* and their frequent preservation in the
198 archaeological record. Sub-sets of landmarks were analysed using PCA, MANOVA
199 and discriminant functions with leave-one-out cross-validation.

200

201 **Measurement Error**

202 Any possible effects of inter-observer error were tested with repeated digitisations
203 following O'Higgins and Jones (1998) and found to be insignificant. The dataset was
204 tested for sexual dimorphism, but no significant variation in shape or size between
205 sexes in either wild or domestic pigs were found, so both sexes were used in the
206 analysis.

207

208 **Modern Proxies**

209 Using modern pigs as proxies for past pig populations could introduce additional
210 sources of error, which must be accounted for if the results are to be applicable to the
211 archaeological record. In this context the possible introgression of Asian pig breeds
212 into European pig breeds must be considered. To minimise this effect, we used older
213 established breeds that have been subject to less improvement (intensive breeding).
214 Theoretically error could also be introduced through interbreeding between wild and
215 domestic animals, contaminating the modern wild sample. However, recent DNA
216 studies have suggested that the amount of Asian DNA from improved modern
217 domesticates is negligible in wild European animals, including pigs, suggesting that
218 there is little contamination from modern domesticates in modern wild populations
219 (Scandura et al., 2011).

220

221

222

223 **Results**

224 **Size differences between Wild vs. Domestic**

225 ANOVA on cranial size differences between wild and domestic individuals is not
226 statistically significant ($p=0.0891$, $df=5$, $F=1.95$). Multivariate regression of shape
227 against log centroid size reveals only a weak positive relationship ($r^2=0.677$, 7.9% of
228 total shape variation explained) between size and shape. No size differences were
229 found between wild and domestic individuals on the basis of any of the cranial
230 subsets.

231

232 **Shape differences between Wild vs. Domestic**

233 Principal components analysis of the complete skull reveals clear morphological
234 differences between wild and domestic pigs, which are completely separated on PC1
235 (58.75% of total variance) with no overlap (figure 1). Wild pigs score positively on
236 PC1 while domestic pigs score negatively. The sample of Tamworth x Wild crosses
237 overlaps with the wild pigs, although they score slightly more negatively than many
238 of the wild pigs. The morphological changes explained by PC1, and subsequently
239 those that separate domestic from wild pigs include a relative straightening of the
240 snout and elongation of the parietal. A one-way MANOVA on shape differences
241 between wild and domestic individuals confirms that there are significant differences
242 between them ($p<0.0001$ $df=625$ $F=6124.91$). In a pair-wise discriminant function
243 with leave-one-out cross-validation (on the first 30 principal components comprising
244 of 95% of total variance), 92% of domestic pigs and 98% of wild pigs were correctly
245 assigned. Distances and discriminant functions were subsequently calculated
246 between wild and domestic individuals on the basis of the landmark sub-sets
247 representing selected regions of the skull (Table 1)

248

249 Relative morphological differences in the cranial sub-sets also show differences
250 between wild and domestic pigs, including a deepening of the angle of the nasal
251 region in domestic pigs - wild pigs having a relatively long straight, narrow snout in
252 contrast to domestic pigs' relatively short, deeply angled and wide snout. The angle
253 of the parietal is more acute in wild pigs (figure 2c) while the angle in domestic pigs
254 is far shallower. When combined with the differences in the nasal, the overall
255 morphology of the parietal is more upright in domestic pigs than wild pigs (figure
256 2b). The zygomatic is relatively more robust in domestic pigs (figure 2d), compared

257 to the slender zygomatic of wild pigs. Features on the underside of the cranium (e.g.
 258 the tympanic bulla) are densely packed in domestic pigs (Figure 2a); while in wild
 259 pigs they are more widely spaced. The PCA plots accompanying the visualisations
 260 (figure 2) show that there is a degree of overlap between wild and domestic
 261 morphologies in the initial PCs of these regions. However table 1 shows that despite
 262 this, there are significant statistical differences between the wild and domestic
 263 morphologies in these regions when the overall pattern of variance is analysed.
 264

Area	Procrustes distance	Mahalanobis' distance	p-value	% Correctly Assigned Domestic	% Correctly Assigned Wild
Whole cranium	0.31822795	18.7093	<.0001	91.7	97.9
Parietal	0.17911991	4.0086	<.0001	88.9	97.9
Nasal	0.08217111	4.0121	<.0001	86.1	97.9
Orbit	0.06971527	2.3496	<.0001	77.8	93.0
Zygomatic	0.12391856	2.9801	<.0001	88.9	94.4
Tooth Row	0.0512221	2.1269	<.0001	72.2	88.0
Basi-cranium	0.13082737	4.0702	<.0001	94.4	95.1

265
 266 Table 1: Procrustes distances and discriminant functions (Mahalanobis' distances)
 267 between wild and domestic samples, *p*-values generated through permutation tests
 268 with 1000 permutations, percentages correctly assigned result from discriminant
 269 functions with leave-one out cross validation. Bolded values highlight results with
 270 high correctly assigned percentages.

271
 272 The results in table 1 and figure 2 demonstrate that both whole and selected regions
 273 of the crania can be used to discriminate between wild and domestic pig
 274 morphologies. The strength of discrimination varies, with the basi-cranium, parietal,
 275 zygomatic and angle of the nasal giving best results. The orbit and tooth row, whilst
 276 correctly assigning most of the wild individuals, misclassify many domestic
 277 individuals, and are not reliable indicators of domestic status.

278

279 **Shape differences between domestic pig breeds**

280 There are significant differences between domestic breeds in both shape (MANOVA
 281 $df=404$ $F=1095.43$ $p<0.0001$) and size (ANOVA $df=4$ $F=7.77$ $p=0.0002$). In a
 282 discriminant function analysis with leave-one-out cross validation the majority of

pigs were correctly assigned to breed (table 2). These results suggest that although the cranial morphology of domesticated pigs may appear similar, it is specific enough to allow statistical discrimination between them.

	Berkshire	Cornwall	Edelschwein	Tamworth- Cross	Tamworth	Veredeltes Landschwein	Wild
Berkshire	80.0	20.0	-	-	-	-	-
Cornwall	-	87.5	-	-	-	12.5	-
Edelschwein	-	12.5	75.0	-	-	12.5	-
Tamworth- Cross	-	-	-	90.0	-	-	10.0
Tamworth	-	-	-	-	80.0	-	20.0
Veredeltes Landschwein	-	7.7	7.7	-	-	84.6	-
Wild	-	-	-	3.0	1.0	-	96

Table 2: Crossvalidation percentage scores of leave-one-out discriminant functions between domestic breeds and wild pigs. Bold values show the percentage correctly assigned to each group. The table should be read from left to right for correct interpretation.

Discussion

Wild and domestic pig crania have distinctly different, quantifiable morphologies. Wild pig crania are more slender, with straighter snouts, whilst domestic pigs have deeply concave snouts and are relatively more robust. These morphological differences have very high supporting discriminant function values, demonstrating that wild and domestic pigs can be separated with a considerable degree of confidence on the basis of cranial morphology. These results are in contrast with the more traditional biometric techniques used in zooarchaeology, which can confidently establish the presence of wild and domestic populations in the archaeological record (Albarella, 2002, Payne and Bull, 1988) but have difficulty distinguishing between populations or assigning wild-domestic status to individuals within those populations. Application of GMM can give well supported and statistically quantifiable results. Additionally we have shown that GMM can differentiate between different pig breeds, which could have significant impact in the study of the origins of domestic animal breeds, and the development of breed improvement.

309 **Partial Crania**

310 Few complete skulls are recovered from archaeological sites, especially in species
311 bred or hunted for human consumption. Breaking the crania into separate
312 components allows us to simulate (to some degree at least) the effects of ante-, peri-
313 and post-mortem taphonomic processes. The parietal, nasal, zygomatic and
314 basicranium provide particularly good discrimination between wild and domestic
315 pigs. In wild pigs the parietal is swept backwards at an acute angle, whereas in
316 domestics the angle is wider as can be seen in the visualisations in figure 2. The nasal
317 region is deeply concave in domestic pigs and flat in the wild boar, whilst the
318 zygomatic is considerably wider and more robust in domestics. On the basicranium,
319 the positions of notable protuberances (such as the pterygoid bone and the tympanic
320 bulla) are crowded together in domestic pigs compared to wild boar. That these areas
321 of the skull exhibit a strong domestic signal compared to others (e.g. the orbit, tooth
322 row), suggests that stresses focused upon specific areas of the crania are important in
323 forming specific domestic morphotypes. These results also suggest that
324 discrimination between wild and domestic morphologies could be possible in
325 fragmented archaeological assemblages.

326

327 **Explaining the changes seen in domestic morphology**

328 Artificial selection, through intensification in breeding and direct selection for
329 specific characters, has produced a far wider variety of morphotypes in domestic
330 animals than exists in their wild progenitors (Drake and Klingenberg, 2010).
331 Domestication also results in unintentional changes to both phenotype and behaviour
332 through modified natural selection in the captive environment and relaxation of
333 selective pressures essential to survival in the wild, and possible changes in the rate
334 and/or pattern of growth during ontogeny (Price, 1999).

335

336 It is possible that some changes in cranial morphology between wild and domestic
337 pigs may be caused by biomechanical strain. Increased muscle use results in
338 increased robusticity in their areas of attachment following Wolff's Law: bone will
339 remodel in response to stress loads placed upon it (Dinu, 2009, Wolff, 1986,
340 O'Regan and Kitchener, 2005). Changes in diet affect the muscles associated with
341 mastication, including the masseter, the temporalis and the pterygoid muscles, in turn
342 affecting the morphology of the parietal fossa, nuchal crest and zygomatic, which we

343 have shown to be more robust in domestic pigs than wild boar. Thus if domestic pigs
344 have a different diet to wild boar, one that requires more processing, it would help
345 explain the morphological changes we have identified. Changes in behaviour,
346 specifically increases in rooting behaviour would also affect cranial morphology.
347 Pigs root for buried food such as roots, tubers and truffles (Sack, 1982). They have a
348 highly developed sense of smell, and a hyper-mobile nasal plate and rostrum with
349 robust muscles (the levator nasolabialis, levator labii superioris, depressor labii
350 superioris) for manipulating the rostrum (Groves, 1981, Sack, 1982, Sisson and
351 Grossman, 1910). Increased rooting would develop the muscles in the nasal and the
352 neck (trapezius) regions exerting greater stress on these points of attachment and
353 modifying their morphology, in ways which could explain the changes observed in
354 the angles of the parietal and nasal. Biomechanical effects on cranial shape do not
355 preclude genetic or other reasons (e.g. stress response, heterochrony) for
356 morphological change, but is an additional factor to be considered when explaining
357 changing morphology during domestication.

358

359 **Cross-bred Wild-Domestic Pigs**

360 One aspect of this study that requires further study is the inclusion of first generation
361 wild (father) x domestic (mother) cross breeds. These animals are from the early
362 stages of the Halle museum breeding experiments and not all the details of their
363 provenance are known, only that they are wild boar crossed with domestic
364 (Tamworth) pigs that were bred at Halle. Their morphological similarity to the wild
365 form suggests that the influence of the domestic signal has been reduced, causing a
366 reversion to a morphotype more similar to that of a wild pig within a single
367 generation. Whether this would be the case if the parentage were reversed is
368 unknown.

369

370 Rapid reversal of domestic morphotypes has also been identified in the genetically
371 inherited coat colour gene, MC1R (Fang et al., 2009), where coat colour is the
372 product of strong positive selection in captivity that quickly reverts to the original
373 wild colour once this selective pressure is removed. Studies of feral animals have
374 suggested that some differences, such as brain size reduction and coat colouration,
375 remain in feral animal morphology (Kruska and Röhrs, 1974, O'Regan and
376 Kitchener, 2005, Zeder, 2012). It is inconclusive whether the causal factor in the

377 retention of domestic phenotype is environmental pressure or the continuation of
378 inherited traits, but our results would suggest that mixture of domestic morphotype
379 with wild removes much of the domestic signature within a generation.

380

381 **Conclusion**

382 Cranial morphology can be used to discriminate between wild and domestic pigs.
383 This is true for both whole and partial crania, as the parietal, zygomatic, angle of the
384 nasal and the basicranium gave excellent discriminant values. The ability to
385 determine between different morphologies, either in cranial or post cranial material
386 has significant implications for zooarchaeology. Greater resolution allows clearer
387 quantification of the proportion of wild and domestic animals on a site, elucidating
388 evolving subsistence strategies and could help determine the origins of the transition
389 from hunter-gathering to farming (Rowley-Conwy et al., 2012).

390

391 The sensitivity of GMM allows for the distinction between domestic breeds. This has
392 important consequences for the study of the origins and development of such breeds,
393 where currently the methodology for studying improvement is based on size
394 increases (Davis et al., 2012), which has obvious difficulties overcoming size issues
395 associated with sexual dimorphism. Breed improvement, for traction or increased
396 meat bearing should be reflected in the morphology, not just size, and could be
397 examined using the methods employed here without being confused with the effects
398 of sexual dimorphism

399

400 Studies have already started applying GMM to zooarchaeological questions and
401 material. Shape differences have been shown to exist between wild and domestic pig
402 teeth in the early archaeological record (Cucchi et al., 2011), and GMM has been
403 applied to both Palaeolithic horse metapodials to investigate phylogeography
404 (Bignon et al., 2005) and cervid anatomy associated with locomotion for palaeo-
405 climatic reconstruction of the Plio-Pleistocene (Curran, 2012). There is great scope
406 for future applications on cranial and post-cranial material, to elucidate both the
407 process and history of domestication.

408

409 **Acknowledgments**

410 This project is supported by NERC (NE/F003382/1) and The Leverhume Trust (F/00
411 128/AX). We thank Frieder Mayer and Saskia Janke at the Museum für Naturkunde
412 Berlin; Renate Schafberg at der Museum für Haüstierkunde, Halle; Alastair
413 Macdonald at the Royal (Dick) School of Veterinary Studies for access to collections
414 and for all their help. We also thank Arden Hulme-Beamen and Linus Girdland-Flink
415 for their contributions.

416

417 **Bibliography**

- 418 ALBARELLA, U. 2002. *Size matters: how and why biometry is still important in*
419 *zooarchaeology*, Oxford, Oxbow Books.
- 420 ARBUCKLE, B. S. 2005. *Experimental Animal Domestication and its Application to*
421 *the Study of Animal Exploitation in Prehistory*, Oxford, Oxbow Books.
- 422 BELYAEV, D. K. 1969. Domestication of Animals. *Science Journal*, 5, 47-&.
- 423 BELYAEV, D. K. 1979. Destablizing selction as a factor in domestication. *Journal*
424 *of Heredity*, 70, 301-308.
- 425 BIGNON, O., BAYLAC, M., VIGNE, J. D. & EISENMANN, W. 2005. Geometric
426 morphometrics and the population diversity of Late Glacial horses in Western
427 Europe (*Equus caballus arcelini*): phylogeographic and anthropological
428 implications. *Journal of Archaeological Science*, 32, 375-391.
- 429 BOOKSTEIN, F. L. 1991. *Morphometric tools for landmark data: geometry and*
430 *biology*, New York, Cambridge University Press.
- 431 CARDINI, A. & ELTON, S. 2009. Geographical and taxonomic influences on
432 cranial variation in red colobus monkeys (Primates, Colobinae): introducing a
433 new approach to 'morph' monkeys. *Global Ecology and Biogeography*, 18,
434 248-263.
- 435 CARDINI, A., JANSSON, A. U. & ELTON, S. 2007. A geometric morphometric
436 approach to the study of ecogeographical and clinal variation in vervet
437 monkeys. *Journal of Biogeography*, 34, 1663-1678.
- 438 CLUTTON-BROCK, J. 1988. *The Walking Larder: Patterns of Domestication,*
439 *Pastoralism and Predation*, London/Boston, Unwin Hyman.
- 440 CUCCHI, T., HULME-BEAMAN, A., YUAN, J. & DOBNEY, K. 2011. Early
441 Neolithic pig domestication at Jiahu, Henan Province, China: clues from
442 molar shape analyses using geometric morphometric approaches. *Journal of*
443 *Archaeological Science*, 38, 11-22.
- 444 CURRAN, S. C. 2012. Expanding ecomorphological methods: geometric
445 morphometric analysis of Cervidae post-crania. *Journal of Archaeological*
446 *Science*, 39, 1172-1182.
- 447 DARWIN, C. 1868. *The Variation of Animals and Plants Under Domestication*
448 London, John Murray.
- 449 DAVIS, S. J. M. 2008. Zooarchaeological evidence for Moslem and Christian
450 improvements of sheep and cattle in Portugal. *Journal of Archaeological*
451 *Science*, 35, 991-1010.
- 452 DAVIS, S. J. M., SVENSSON, E. M., ALBARELLA, U., DETRY, C.,
453 GOTHERSTROM, A., PIRES, A. E. & GINJA, C. 2012. Molecular and
454 osteometric sexing of cattle metacarpals: a case study from 15th century AD
455 Beja, Portugal. *Journal of Archaeological Science*, 29, 1445-1454.

- 456 DINU, A. 2009. The action of the masticatory muscles and cranial changes in pigs as
457 results of domestication. *Documenta Praehistorica*, 36, 207-218.
- 458 DRAKE, A. G. 2011. Dispelling dog dogma: an investigation of heterochrony in
459 dogs using 3D geometric morphometric analysis of skull shape. *Evolution &*
460 *Development*, 13, 204-213.
- 461 DRAKE, A. G. & KLINGENBERG, C. P. 2010. Large-Scale Diversification of
462 Skull Shape in Domestic Dogs: Disparity and Modularity. *American*
463 *Naturalist*, 175, 289-301.
- 464 ERVYNCK, A., DOBNEY, K., HONGO, H. & MEADOW, R. 2001. Born Free?
465 New Evidence for the Status of *Sus scrofa* at Neolithic Çayönü Tepesi
466 (Southeastern Anatolia, Turkey). *Paléorient* 27, 47-73.
- 467 EVAN TOOLBOX. 2010. <http://evan-society.org/node/42> [Online].
- 468 FANG, M., LARSON, G., RIBEIRO, H. S., LI, N. & ANDERSSON, L. 2009.
469 Contrasting Mode of Evolution at a Coat Color Locus in Wild and Domestic
470 Pigs. *PLOS Genetics*, 5. 1. e1000243
- 471 GOULD, S. J. 1977. *Ontogeny and Phylogeny*, Cambridge MA, The Belknap Press
472 of Harvard University Press.
- 473 GROVES, C. 1981. *Ancestors for the Pigs: Taxonomy and Phylogeny of the Genus*
474 *Sus*, Canberra, Research School of Pacific Studies, Australian National
475 University.
- 476 HARE, B., WOBBER, V. & WRANGHAM, R. 2012. The self-domestication
477 hypothesis: evolution of bonobo psychology is due to selection against
478 aggression. *Animal Behaviour*, 83, 573-585.
- 479 KLINGENBERG, C. P. 2008. *Morphoj* [Online]. University of Manchester, UK.:
480 Faculty of Life Sciences. Available:
481 http://www.flywings.org.uk/MorphoJ_page.htm.
- 482 KOVAROVIC, K., AIELLO, L. C., CARDINI, A. & LOCKWOOD, C. A. 2011.
483 Discriminant function analyses in archaeology: are classification rates too
484 good to be true? *Journal of Archaeological Science*, 38, 3006-3018.
- 485 KRUSKA, D. & RÖHRS, M. 1974. Comparative-quantitative investigations on
486 brains of feral pigs from the Galapagos Islands and the European domestic
487 pig. *Zeitschrift für Anatomie und Entwicklungsgeschichte*, 144, 61-73.
- 488 KÜNZL, C., KAISER, S., MEIER, E. & SACHSER, N. 2003. Is a wild mammal
489 kept and reared in captivity still a wild animal? *Hormones and Behavior*, 43,
490 187-196.
- 491 LYMAN, R. L. 1994. *Vertebrate Taphonomy (Cambridge Manuals in Archaeology)*
492 Cambridge, Cambridge University Press.
- 493 MAYER, J. J., NOVAK, J. M. & BRISBIN JR., I. L. 1998. Evaluation of Molar Size
494 as a Basis for distinguishing Wild Boar from Domestic Swine: Employing the
495 Present to Decipher the Past. In: NELSON, S. M. (ed.) *Ancestors for the*
496 *Pigs: Pigs in Prehistory*. Philadelphia: Museum Applied Science Centre for
497 Archaeology.
- 498 MEIRI, S. & DAYAN, T. 2003. On the validity of Bergmann's rule. *Journal of*
499 *Biogeography*, 30, 331-351.
- 500 MITTEROECKER, P. & GUNZ, P. 2009. Advances in Geometric Morphometrics.
501 *Evolutionary Biology*, 36, 235-247.
- 502 MITTEROECKER, P., GUNZ, P. & BOOKSTEIN, F. L. 2005. Heterochrony and
503 geometric morphometrics: a comparison of cranial growth in *Pan paniscus*
504 versus *Pan troglodytes*. *Evolution & Development*, 7, 244-258.

- O'HIGGINS, P. 2000. The study of morphological variation in the hominid fossil record: biology, landmarks and geometry. *Journal of Anatomy*, 197, 103-120.
- O'HIGGINS, P. & JONES, N. 1998. Facial growth in *Cercocebus torquatus*: an application of three-dimensional geometric morphometric techniques to the study of morphological variation. *Journal of Anatomy*, 193, 251-272.
- O'REGAN, H. J. & KITCHENER, A. C. 2005. The effects of captivity on the morphology of captive, domesticated and feral mammals. *Mammal Review*, 35, 215-230.
- PAYNE, S. & BULL, G. 1988. Components of variation in measurements of pig bones and teeth, and the use of measurements to distinguish wild from domestic pig remains. *ArchaeoZoologia*, 2, 27-65.
- PRICE, E. O. 1984. Behavioural-aspects of animal domestication. *Quarterly Review of Biology*, 59, 1-32.
- PRICE, E. O. 1999. Behavioral development in animals undergoing domestication. *Applied Animal Behaviour Science*, 65, 245-271.
- ROHLF, F. J. 2003. Bias and error in estimates of mean shape in geometric morphometrics. *Journal of Human Evolution*, 44, 665-683.
- ROSENBERG, M. & REDDING, R. W. 1998. Early Pig Husbandry in Southwestern Asia and Its Implications for Modeling the Origins of Food Production. In: NELSON, S. M. (ed.) *Ancestors for the Pigs: Pigs in Prehistory*. Philadelphia: Museum Applied Science Centre for Archaeology (MASCA).
- ROWLEY-CONWY, P., ALBARELLA, U. & DOBNEY, K. 2012. Distinguishing Wild Boar from Domestic Pigs in Prehistory: A Review of Approaches and Recent Results. *Journal of World Prehistory*, 25, 1-44.
- SACK, W. O. 1982. *Essentials of Pig Anatomy: Horowitz/Kramer Atlas of Musculoskeletal Anatomy of the Pig*, Ithaca, New York, Veterinary Textbooks.
- SCANDURA, M., IACOLINA, L. & APOLLONIO, M. 2011. Genetic diversity in the European wild boar *Sus scrofa*: phylogeography, population structure and wild x domestic hybridization. *Mammal Review*, 41, 125-137.
- SISSON, S. & GROSSMAN, J. D. 1910. *The Anatomy of the Domestic Animals*, Philadelphia and London, W. B. Saunders and Company.
- TRUT, L. N. 1999. Early canid domestication: The farm-fox experiment. *American Scientist*, 87, 160-169.
- VIGNE, J.-D., HELMER, D. & PETERS, J. 2005. New archaeological approaches to trace the first steps of animal domestication: general presentation, reflections and proposals. In: VIGNE, J. D., PETERS, J. & HELMER, D. (eds.) *First Steps of Animal Domestication: New Archaeological Approaches*. Oxford: Oxbow Books.
- VIGNE, J. D. 2011. The origins of animal domestication and husbandry: A major change in the history of humanity and the biosphere. *Comptes Rendus Biologies*, 334, 171-181.
- VON DEN DRIESCH, A. 1976. *A Guide to the Measurement of Animal Bones from Archaeological Sites*, Cambridge, MA, Peabody Museum Bulletin 1.
- WOLFF, J. 1986. *The Law of Bone Remodeling (translation of the German 1892 edition)*, New York, Springer.
- ZEDER, M. 2012. Pathways to Animal Domestication. In: GEPTS, P., FAMULA, T. R., BETTINGER, R. L., BRUSH, S. B., DAMANIA, A. B., MCGUIRE, P. E. & QUALSET, C. O. (eds.) *Biodiversity in Agriculture: Domestication, Evolution, and Sustainability*. Cambridge: Cambridge University Press.

555 ZEDER, M. A. 2006. Archaeological Approaches to Documenting Animal
 556 Domestication. In: ZEDER, M. A., BRADLEY, D., ERMSHWILLER, E., &
 557 SMITH, B. D. (eds.) *Documenting Domestication: New Genetic and*
 558 *Archaeological Paradigms*. Berkeley, Los Angeles, London: University of
 559 California Press.
 560 ZELDITCH, M. L., DONALD, L., SWIDERSKI, H., SHEETS, D. & FINK, W. L.
 561 2004. *Geometric Morphometrics for Biologists: A Primer*, London, Elsevier
 562 Academic Press.
 563 ZEUNER, F. E. 1963. *A History of Domestic Animals*, London, Hutchinson & Co.

564
 565 **Figure 1:** PCA of wild and domestic pigs

566 **Figure 2:** PCA of subsections of the suid crania, 2a: basicranium, 2b: nasal region,
 567 2c: parietal, 2d: zygomatic.

568

569 **Figure 1**

570

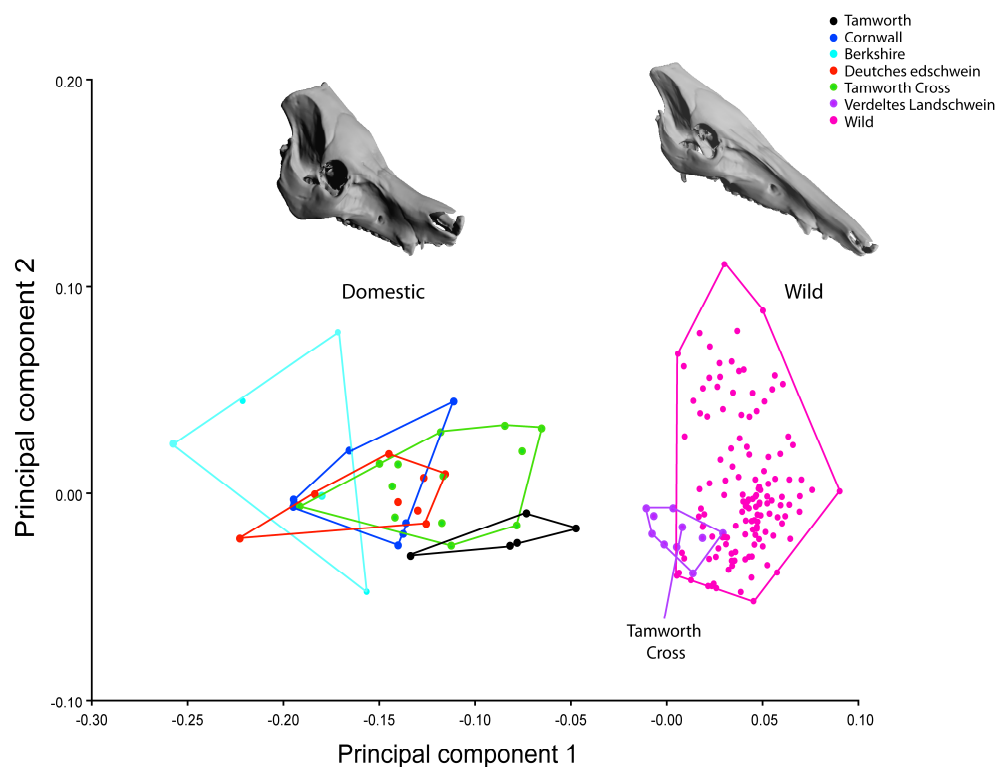


Figure 1: PCA of Wild and domestic pigs.
 PC1=58.746% of total variance, PC2=9.961%

571

572

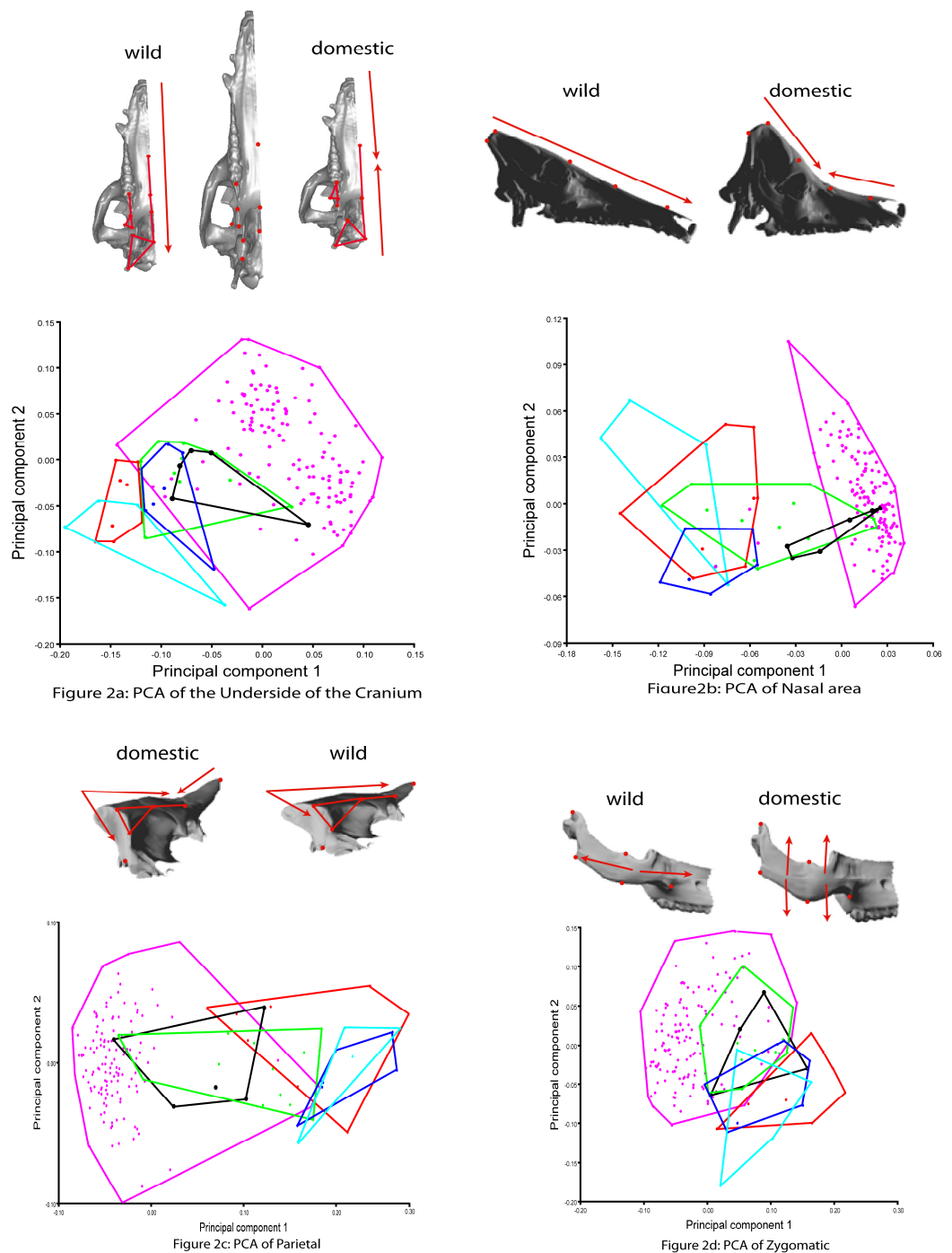


Figure 2: PCAs of sub-sections of the cranium: showing separation of wild and domestic pigs

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16

Chapter 6
Manuscript 4

Domestication and Heterochrony in *Sus scrofa*

Title: Domestication and Heterochrony in *Sus scrofa*

Joseph OWEN^{a,b}, Kieran MCNULTY^c, Keith DOBNEY^d, Greger LARSON^e, and Una STRAND VIDARSDOTTIR^b.

^aDepartment of Archaeology, Durham University, South Road, Durham DH1 3LE, United Kingdom j.t.d.owen@dur.ac.uk;

^bDepartment of Anthropology, Durham University, South Road, Durham DH1 3LE, United Kingdom una.vidarsdottir@durham.ac.uk

^cDepartment of Anthropology, University of Minnesota, 395 Humphrey Center, 301 19th Ave S, Minneapolis, MN 55455, USA kmcnulty@umn.edu

^dDepartment of Archaeology, University of Aberdeen, St.Mary's Building, Elphinstone Road, AB24 3UF, United Kingdom keith.dobney@abdn.ac.uk

^eDurham Evolution and Ancient DNA Lab, Department of Archaeology, Durham University, South Road, Durham DH1 3LE, United Kingdom greger.larson@durham.ac.uk

Abstract

Domestication creates a variety of unique animal morphologies and behaviours. Traditionally these have been explained through the frame work of heterochrony: changes in the rate and timing of development. The domestic phenotype is often described as paedomorphic, resembling the juvenile ancestral state. Recent advances in techniques like Geometric Morphometrics (GM) have falsified hypotheses of paedomorphism in dogs (Drake, 2011), and examined cranial heterochrony in hominids and monkeys. Here we examine the theory of heterochrony being responsible for the development of domestic phenotype in pigs (*Sus scrofa*). We apply GM methods to 3 longitudinal ontogenetic series (one wild, two domestic), calculating the angles between ontogenetic trajectories and comparing morphological distances between the series at different ages. We also test wild and domestic pigs for evidence of paedomorphism. We conclude that heterochrony is not sufficient to explain the domestic morphology of pigs, nor is there evidence of paedomorphism in 5 of the 6 domestic breeds tested. Thus the traditional explanation of heterochrony as the causal mechanism for the domestic phenotypic is incorrect, and a new explanation must be sought.

51

52 **Introduction**

53 Domestication can cause radical morphological change in animals. Examples include
54 reduction of cranial capacity, alterations to cranial size and shape, changes in body
55 mass, changes in pelage colour and density, and changes to dentition and behavioural
56 modifications (Bokonyi, 1974, Price, 1999, Zeder, 2012). These changes can occur
57 rapidly and are seen in a wide variety of animals where the only commonality is
58 some form of 'domestication'. There is some evidence for these changes being
59 interlinked. In an experiment of domesticating foxes in Russia (Belyaev, 1979) the
60 sole selection factor applied to a population of captive foxes was reduced aggression
61 towards the human handlers (Belyaev, 1979, Trut, 1999). Within 8-10 generations
62 this caused significant changes in morphology, including increases in the proportion
63 of the fox population exhibiting floppy ears; piebald coat colouring, shortened,
64 curled tails, submissive posturing, tail wagging and increased vocality towards
65 humans. These changes in morphology and behaviour were thought to be linked to
66 changes in the adrenal cortex and other hormone regulatory systems (Trut, 1999,
67 Trut et al., 2009).

68

69 The changes associated with the domestic phenotype are traditionally explained as
70 being paedomorphic, i.e. retaining the juvenile morphology or behaviour into
71 adulthood (Moray, 1992, 1994, Price, 1999, Zeder, 2012). Paedomorphism is caused
72 by heterochrony, the evolutionary process that generates diversity via changes in the
73 rate or timing of ontogenetic pathways (Alberch et al., 1979). Gould (1977)
74 described three components of ontogeny - age, size and shape. The evolutionary
75 disassociation of these three components during ontogeny can produce a descendent
76 morphology that either resembles the ancestral morphology at a younger stage of
77 development (paedomorphosis) or at a continued stage of development
78 (peramorphosis) (Alberch et al., 1979). Paedomorphism can arise from either the
79 mechanisms of neoteny, slowing the growth rate of shape relative to age; progenesis,
80 reducing the period of growth in shape, resulting in early sexual maturity; and post
81 displacement, where shape growth occurs later (Godfrey and Sutherland, 1995). It is
82 neoteny that is often invoked to explain the divergent morphology of domestic
83 animals. However, closer examination of the cranial characteristics of dogs (Drake,
84 2011) has shown that they do not share the morphological characteristics of adult or

85 juvenile wolves, and that the vast range of phylogenetically novel dog skull shapes
86 does not coincide with the expectations of the heterochronic model. This leaves the
87 model of morphological change in domestic animals uncertain. In this study we
88 analyse and compare ontogenetic pathways of wild and domestic pigs as well as
89 assessing the hypothesis of paedomorphism, aiming to test whether the heterochrony
90 really can explain the morphological changes caused by domestication.

91
92 Geometric Morphometrics is an ideal method for examining ontogeny as it allows a
93 detailed analysis of shape independent of size, and provides a platform for a
94 multivariate statistical analysis whereby the interactions of age, size and shape can be
95 determined. Drake's study of dog morphology used GMM techniques to successfully
96 refute paedomorphism as a cause of morphological variation in domestic canids
97 (Drake, 2011). It has been used successfully to analyse ontogeny in other species,
98 where it has revealed that closely related species and individual populations within a
99 species can develop along very different ontogenetic trajectories. For example
100 Viðarsdóttir and Cobb (2004) demonstrated that for four species of apes: *Homo*
101 *sapiens*, *Gorilla gorilla*, *Pan troglodytes* and *Pan paniscus*, closely related genera, or
102 members of the same genus, do not share a common early post-natal ontogeny.
103 Ontogenetic divergence can also be seen intra-specifically, in *H. sapiens* differences
104 present at birth are accentuated and modified during growth to produce distinct facial
105 morphologies in geographically distinct human populations (Viðarsdóttir et al.,
106 2002). GMM has also been used to test hypotheses of heterochrony. Mitteroecker et
107 al. (2004) used GMM to show that the differences in facial form between *H.sapiens*,
108 *P. troglodytes* and *G. Gorilla* are most likely genetically controlled, and that suggest
109 pure heterochrony can not explain the subsequent further divergence in cranial form.
110 Heterochrony is also rejected as the causal mechanism for inter-specific differences
111 in chimpanzee skulls (*P. paniscus* and *P. troglodytes*), a hypothesis that was often
112 invoked to explain allometric scaling in hominid evolution (Mitteroecker et al.,
113 2005). It has also been falsified as the cause of intra-specific sexual dimorphism in
114 *Alouatta palliata* (Howler Monkeys) (Blanco and Godfrey, 2006).

115

116 It is unlikely that heterochrony affects the skull globally, as it has been shown that
117 the cranium is developmentally modular (Mitteroecker and Bookstein, 2007, 2008),
118 and independent evolution of different regions of the skull does not necessarily result

119 in a global growth pattern or global heterochrony. Instead, regional development can
120 exist as localised allometric scaling (David, 1990) or ‘dissociated’ heterochrony
121 (McKinney and McNamara 1991). It is difficult to determine whether different
122 regions are undergoing independent heterochrony (Mitteroecker et al., 2005), so we
123 attempt a broad approach examining two modules of the crania, the facial region and
124 the neurocranium.

125

126 The pig (*Sus scrofa* L.1758) is a crucial food and economic resource in both its wild
127 and domestic form. Pigs have a long standing affiliation with humans, hunted for
128 their meat before the Pleistocene (Albarella et al., 2007) and first domesticated in
129 South-Eastern Anatolia around 10,500BP (Zeder, 2008). From there domesticated
130 pigs spread throughout Europe and North Africa (Larson et al., 2007), with
131 additional separate domestication events in both Europe (Larson et al., 2005b) and
132 China (Cucchi et al., 2011). It is now one of the most widespread terrestrial
133 mammals on the planet, found on all the inhabited continents either through natural
134 or human aided dispersal (Groves, 1981, Grubb, 2005). Pigs have a demonstrable
135 morphological response to domestication, including cranial modification (Bokonyi,
136 1974), body mass reduction (Ervynck et al., 2001) and changes to coat colour (Fang
137 et al., 2009), making them an ideal subject to test for heterochrony. Pigs are also well
138 suited for a test of paedomorphism, as the domestic pigs direct ancestral population
139 survives today in the form of the European wild boar (Larson et al., 2005a, 2007).

140

141 **Materials**

142 Three longitudinal ontogenetic series were examined in this study, a single wild
143 series composed of 32 individuals and two domestic series, composed of 17
144 Berkshire pigs and 25 Deutsches Edeschwein pigs. The wild pigs were from Poland,
145 mainly the Białowiecki National Park, but also some from South-West Poland near
146 Nysa, all collected in the Natural History Museum in Berlin. The domestic pigs were
147 digitised at the Julius Kühn Museum of Domestication in Halle, East Germany,
148 where they were also raised. Ontogenetic series of individual breeds or wild animals
149 were taken from the same geographic area to reduce the effects of environmental
150 factors. Complete ontogenetic sequences are rare, hence the use of an incomplete
151 ontogenetic sequence in the Berkshire pigs (containing only two very young
152 individuals) and the preliminary nature of this investigation.

153

154 The pigs were divided into three age stages based on dental characteristics: age stage
155 1 represents neonatal to two months; stage 2 three to fifteen months; and age stage 3
156 sixteen months and older. The wild pigs were aged according to tooth eruption
157 following the protocol of Higham (1967). The exact birth and death dates were
158 available the majority of the domestic individuals, the remainder were aged
159 following the same protocol as the wild pigs. All pigs, wild and domestic, were split
160 into the age stages using the Higham protocol for consistency (which assigned the
161 domestic pigs of known age correctly).

162

163 The ontogenetic series was further split into two subsets, the face and neurocranium,
164 to test the hypothesis of regional heterochrony. See table S1 for landmark details.

165

166 To test for pedomorphism the wild ontogenetic series was compared to a variety of
167 adult domestic pigs, including Deutsches Edelschwein (9 individuals), Hannover-
168 Braunschweig-Landschwein (3), Tamworth (5), Veredeltes Edelschwein (13),
169 Cornwall (8) and Berkshire pigs (5).

170

171 **Methods**

172 Thirty-eight unilateral three-dimensional coordinates (Supporting Table S1) were
173 digitised from the right side of the cranium, using a Microscribe® GLS
174 (EMicroscribe Inc), by the first author. Specimens were standardised using
175 Generalised Procrustes Analysis (GPA) (Bookstein, 1991, Mitteroecker and Gunz,
176 2009, Rohlf, 2003) and morphological relationships explored using Principal
177 Component Analyses (PCA). Significance of differences in shape between groups
178 was assessed using Multivariate Analysis of Variance (MANOVA). Mahalanobis'
179 and Procrustes distances between group means (tested with 10,000 permutations)
180 were compared to examine the similarity/dissimilarity of shape between samples
181 (Drake, 2011). Digitising and methodological error was assessed following
182 O'Higgins and Jones (1998) and found to be negligible.

183

184 To investigate heterochrony taking into account size, shape and age, a multivariate
185 analysis of shape using Geometric Morphometrics (GM) can be used to plot the
186 ontogenetic trajectories of ancestral and descendant population through principal

187 components analysis. If the trajectories differ without overlap heterochrony can be
188 rejected, if they overlap, it can be accepted. In a multivariate shape analysis overlap
189 in the initial PCs is no guarantee of overlapping trajectories in wider shape space. To
190 account for this a within group multivariate regression of shape on log size with
191 permutation tests was computed for each sample within a multidimensional shape
192 space with the origins centred. The angle between the ontogenetic trajectories of wild
193 and domestic samples was determined to prove or disprove heterochrony
194 (Mitteroecker et al., 2005).

195

196 To test for paedomorphism in pigs, the adult descendant morphology (here
197 represented by domestic pigs) is compared to different ages of the ancestral
198 morphology (wild pigs). To support a hypothesis of paedomorphism, the descendent
199 morphology should be closer in shape to the young or juvenile ancestral morphology
200 than to the adult ancestral morphology. If the adult descendant populations are
201 further from the juvenile ancestral populations the hypothesis of paedomorphism will
202 be rejected. To test the hypothesis the Mahalanobis' and Procrustes distances
203 between a variety of adult domestic pig breeds and the wild ontogenetic series were
204 computed and tested with 10,000 permutations.

205

206 To test for regional ontogeny the sub-sets of data for the neurocranium and the facial
207 region of the cranium (see supporting table S2) were subjected to the same tests as
208 the whole cranium. Distances were calculated and compared between wild and
209 domestic datasets, and the ontogenetic trajectories and the angles between them
210 computed. All analyses were carried out in Morphologika (O'Higgins and Jones,
211 2006), MorphoJ (Klingenberg, 2008) and SAS.

212

213 **Results**

214 **Differences between complete wild and domestic pig crania**

215 Differences in shape between the wild and domestic groups, including all age stages
216 were tested with MANOVA and found to be significantly different ($p < 0.0001$,
217 $df=214$, $F=6441.26$), demonstrating that all three groups are morphologically distinct
218 from one another. The morphological distances between groups (table 1) confirm the
219 MANOVA result: the groups are all distinct from one another. Table 1 also shows
220 that the domestic pig groups are closer, and thus more similar to each other in shape,

221 than either is to the wild pig group. These cranial shape differences between wild and
 222 domestic pigs are summarised through PCA (Figure 1). The first PC separates the
 223 domestic and wild morphologies (48.3% of total variance). The second PC (29.8% of
 224 total variance) shows ontogenetic trajectories, where the youngest and smallest pigs
 225 score lowest and the older pigs score highest. As the pigs age the ontogenetic
 226 trajectories between wild and domestic pigs diverge along PC1, so older pigs are at
 227 the extremes of PC1 and the younger pigs cluster in the middle.
 228

Distance Between	Mahalanobis distance	<i>p</i> -value	Procrustes Distance	<i>p</i> -value
Edelschwein-Berkshire	9.5839	<0.0001	0.044	0.17
Edelschwein-Wild	13.3303	<0.0001	0.1559	<0.0001
Berkshire-Wild	14.5291	<0.0001	0.1808	<0.0001

229 **Table 1:** Distances between wild and domestic groups, for the complete crania for all ages.

230

231 When the groups were broken down into the age classes there were still significant
 232 differences between them at all ages, but the differences between the wild and
 233 domestic pigs increase with age. Table 2 (below) shows the distances between the
 234 age groups. At all age stages the distance between the domestic groups is less than
 235 the distance between wild and domestic pigs. The distances are smaller at age stage 1
 236 than age stage 2 or 3.

237

Distance Between	Mahalanobis distance	<i>p</i> -value	Procrustes Distance	<i>p</i> -value
Age Stage 1 (0-2 months) group size = 17				
Edelschwein-Berkshire	7.0183	0.018	0.1604	0.015
Edelschwein-Wild	8.5019	<0.0001	0.1612	<0.0001
Berkshire-Wild	12.3636	0.005	0.2362	0.026
Age Stage 2 (3-15 months) group size = 31				
Edelschwein-Berkshire	10.4971	<0.0001	0.0987	<0.0001
Edelschwein-Wild	18.7865	<0.0001	0.3415	<0.0001
Berkshire-Wild	18.8497	<0.0001	0.3914	<0.0001
Age Stage 3 (15+ months) group size = 24				
Edelschwein-Berkshire	6.8572	<0.0001	0.1316	<0.0001
Edelschwein-Wild	15.5797	<0.0001	0.4148	<0.0001

Berkshire-Wild	18.4329	<0.0001	0.4537	<0.0001
----------------	---------	---------	--------	---------

Table 2: Morphological distances between complete pig crania at different ages.

Differences between ontogenetic trajectories

Angle of Trajectories Between	Angle Degree(°)	p-value
Edelschwein-Berkshire	29.747	n/a
Edelschwein-Wild	44.032	0.062
Berkshire-Wild	54.63	n/a

Table 3: Angle between ontogenetic trajectories

Table 3 (above) shows pair wise angles between the ontogenetic trajectories of the wild and domestic groups. The angle between the domestic breeds is smaller than the angle between the domestic and wild pigs; thus the domestic pigs are on a similar but not identical ontogenetic trajectory to each other, one that is different to the wild pigs. Permutation tests were not possible with the Berkshire group as there were not enough individuals in age stage 1, and the permutation test between the Deutsches Edelschwein and wild pigs returned a non-significant result, which is also linked to small sample sizes and the resulting low statistical power of the test.

Tests for paedomorphism

Distance Between	Mahalanobis distance	p-value	Procrustes distance	p-value
Wild Stages vs. Deutsches Edeschwein Adult (#9)				
Stage 1	7.9302	<.0001	0.2098	<.0001
Stage 2	9.1212	<.0001	0.2057	<.0001
Stage 3	8.2867	<.0001	0.2065	<.0001
Wild Stages vs. Berkshire Adult (#5)				
Stage 1	4.2620	<.0001	0.1957	<.0001
Stage 2	7.7199	<.0001	0.2031	<.0001
Stage 3	8.5302	<.0001	0.2109	<.0001
Wild Stages vs. Hannover-Braunschweig-Landschwein Adult (#3)				
Stage 1	6.2993	0.0100	0.2016	0.0060
Stage 2	10.2571	0.0020	0.1769	0.0010
Stage 3	6.2472	<.0001	0.1719	0.0010
Wild Stages vs. Tamworth Adult (#5)				
Stage 1	6.8805	0.0100	0.1803	<.0001
Stage 2	6.7945	<.0001	0.1045	<.0001
Stage 3	3.6291	<.0001	0.0907	<.0001
Wild Stages vs. Veredeltes Edelschwein Adult (#13)				
Stage 1	9.7828	<.0001	0.1759	<.0001
Stage 2	6.3832	<.0001	0.1396	<.0001
Stage 3	3.8714	<.0001	0.1400	<.0001
Wild Stages vs. Cornwall Adult (#8)				

Stage 1	7.7208	<.0001	0.2163	<.0001
Stage 2	12.8338	<.0001	0.2025	<.0001
Stage 3	10.1080	<.0001	0.1991	<.0001

Table 4: Tests for paedomorphism, morphological distances between the three ages stages of the wild group and different adult domestic pigs

For the hypothesis of paedomorphism to be true the adult descendent population (domestic pigs) must resemble the juvenile morphology of the ancestral population (wild pigs), i.e. it must be closer in morphological distances to wild stage 1 than to wild stage 3. The tests for paedomorphism (table 4) return negative results for Deutsches Edeschwein, Hannover-Braunschweig-Landschwein, Tamworth and Veredeltes Edelschwein. These adult pigs are either at similar distances or greater distances from wild age stage 1 than from wild age stage 3. The result for the Cornwall pigs gives an ambiguous result, the Mahalanobis distance suggests that adult Cornwall pigs are paedomorphic, but the procrustes distance does not. This may be due to Mahalanobis distances being a product of discriminant function, and thus not scaling directly as a true biological distance, unlike the procrustes distances which reflect the shape differences between samples. The result for the Berkshire pigs returns a positive result, suggesting that Berkshire pigs are possibly paedomorphic.

Partial crania

Distance Between	Mahalanobis distance	p-value	Procrustes distance	p-value
Partial Crania				
Neurocranium				
Edelschwein-Berkshire	17.935	<0.0001	0.0875	<0.0001
Edelschwein-Wild	37.8219	<0.0001	0.2299	<0.0001
Berkshire-Wild	38.9994	<0.0001	0.2646	<0.0001
Facial				
Edelschwein-Berkshire	9.1617	<0.0001	0.0967	<0.0001
Edelschwein-Wild	18.9819	<0.0001	0.3047	<0.0001
Berkshire-Wild	20.337	<0.0001	0.3414	<0.0001

Table 5: Distances in shape space between wild and domestic groups; within the whole crania and partial crania (neurocranium and face); also the distances between age stages between groups.

In the analysis of the partial cranium, both the neurocranium and the face reflect the results of the whole crania. The distances between the two domestic groups are much smaller than the distances between the wild and domestic groups. The neurocranial distances between the groups are larger than those for the face or the whole cranium,

perhaps suggesting that the neurocranium is more morphologically distinct between wild and domestic groups than is the face.

280

281 Ontogenetic angles of partial crania

Neurocranium Angle of Trajectories Between	Angle Degree(°)	p-value
Edelschwein-Berkshire	24.843	n/a
Edelschwein-Wild	27.584	n/a
Berkshire-Wild	34.615	n/a
Facial Angle of Trajectories Between	Angle Degree(°)	p-value
Edelschwein-Berkshire	25.343	n/a
Edelschwein-Wild	28.806	n/a
Berkshire-Wild	33.990	n/a

282

Table 6: Angles between ontogenetic trajectories for the partial crania.

283 Comparison of the ontogenetic trajectories for different regions of the cranium
 284 reveals that the angles between the domestic and wild pigs are larger than the angles
 285 between the two domestic groups, mimicking the result for the complete crania. The
 286 angles involved are smaller than the angles of the complete crania, most likely due to
 287 the reduced dimensionality of the dataset (as a result of the reduced number of
 288 landmarks).

289

290 Discussion

291 The cranial morphologies of wild and domestic pigs are distinct, at birth, in
 292 adulthood and at all stages in between. Their ontogenetic trajectories diverge, the
 293 distances between wild and domestic pigs increasing as the pigs age. This is
 294 demonstrated clearly in Figure 1, on PC1 the young wild and domestic pigs are close
 295 together, but the adult wild and domestic populations are far apart. This pattern is
 296 supported by the Mahalanobis and Procrustes distances between the domestic breeds
 297 and the wild pigs at all age stages (Table 3). While young (age group 1) the distances
 298 between the wild group and the two domestic groups are small, although young
 299 Deutsches Edelschwein are closer to wild piglet shape than are young Berkshire pigs.
 300 The older age groups (2 and 3) show the distances between the domestic pigs are
 301 small and the distance between wild-domestic pigs is large, the shapes are distinctly
 302 different. We are able to infer from these results that post-natal ontogeny is
 303 responsible for much of the adult cranial morphology in pigs, but that pre-natal
 304 growth has already established significant differences between wild and domestic
 305 cranial form at age stage 1.

306

307 A multivariate shape analysis of cranial ontogenetic trajectories produces three
308 different trajectories from three groups, with wild pigs further separated from the two
309 domestic trajectories. According to Mitteroecker et al. (2005) heterochrony is a
310 sufficient descriptor of morphological change only if the same morphological
311 processes are responsible for change, but differently timed. If the ontogenetic
312 trajectories in shape space differ the theory of heterochrony is falsified. Differences
313 in the angle of ontogenetic trajectories between wild and domestic pigs show that
314 heterochrony is not likely to be responsible for the observed morphological change.
315 Even though the sample size was very small, a p -value not far from significance
316 (0.062) was returned. Larger samples may rectify this problem.

317

318 The tests for paedomorphism show that the majority of the pig breeds are not
319 paedomorphic; the descendant populations (the domestic pigs) are not closer to the
320 young ancestral (wild) population than the adult ancestral population. The exception
321 is the Berkshire pig, which does satisfy these criteria for paedomorphism. Overall,
322 paedomorphism is not a sufficient descriptor of the changes seen in domestic pigs,
323 although these results suggest that pig breeds respond differently to domestication,
324 and the ontogenetic angles between the domestic breeds confirm this.

325

326 Both the neurocranium and face of the pig show significant differences in
327 morphology between wild and domestic pigs. As in the complete cranium there are
328 greater distances between the wild and domestic groups, than between the two
329 domestic groups. The ontogenetic trajectories are also distinct between all groups.
330 There is no evidence of modular heterochrony in our analysis as the regional data
331 mirrors the results for the whole crania. Note this does not completely rule out
332 modular heterochrony, as it could be taking place on a smaller scale than tested for.
333 However to determine this would require more detailed analysis (a greater number of
334 landmarks) on larger datasets, which are unavailable at this time.

335

336 **Conclusion**

337 Heterochrony is not the basis of the domestic phenotype, nor are most domestic pigs
338 paedomorphic. This paper thus joins a series of others rejecting heterochrony as the
339 causal mechanism for morphological change in a host of animals; including dogs

340 (Drake, 2011), chimpanzees (Mitteroecker et al., 2005) and howler monkeys (Blanco
341 and Godfrey, 2006). However, in the literature of domestication heterochrony is still
342 evoked as the underlying mechanism of morphological change (Zeder, 2012, Hare et
343 al., 2012). Although paedomorphic behavioural characters in domestic animals have
344 been identified (Coppinger et al., 1987, Moray, 1992, Moray, 1994, Trut et al.,
345 2009), morphological characters classified as paedomorphic cannot be quantified in
346 either pigs or dogs.

347

348 If heterochrony is not the causal mechanism for morphological change in domestic
349 animals then what is? Clearly there is some pre- or post-natal mechanism or process
350 that is enforcing changes to morphology, yet the traditional language of heterochrony
351 appears inadequate to explain it. We must also keep in mind that the processes acting
352 prenatally may not be the same as those acting postnatally. Further definition of the
353 changes that occur during growth and development may help answer this question.
354 Analysis of other domesticates, like horses, sheep or cattle may show commonalities
355 in the development of domestication. There are experiments that manipulate the
356 conditions of growth in domestic animals e.g. the fox farm experiment by Belyaev
357 (Belyaev, 1979, Trut, 1999) or various experiments on mice or rats (Arbuckle, 2005).
358 Multivariate analysis of the crania of the specimens in those experiments would
359 allow specific links to be drawn between morphological development, hormone
360 fluctuation and the genetic mechanisms behind them.

361

362 **Acknowledgements**

363 This project is supported by NERC (NE/F003382/1) and The Leverhume Trust (F/00
364 128/AX). We thank Frieder Mayer and Saskia Janke at the Museum für Naturkunde
365 Berlin and Renate Schafberg at der Museum für Haustierkunde, Halle for access to
366 their collections and all their help.

367

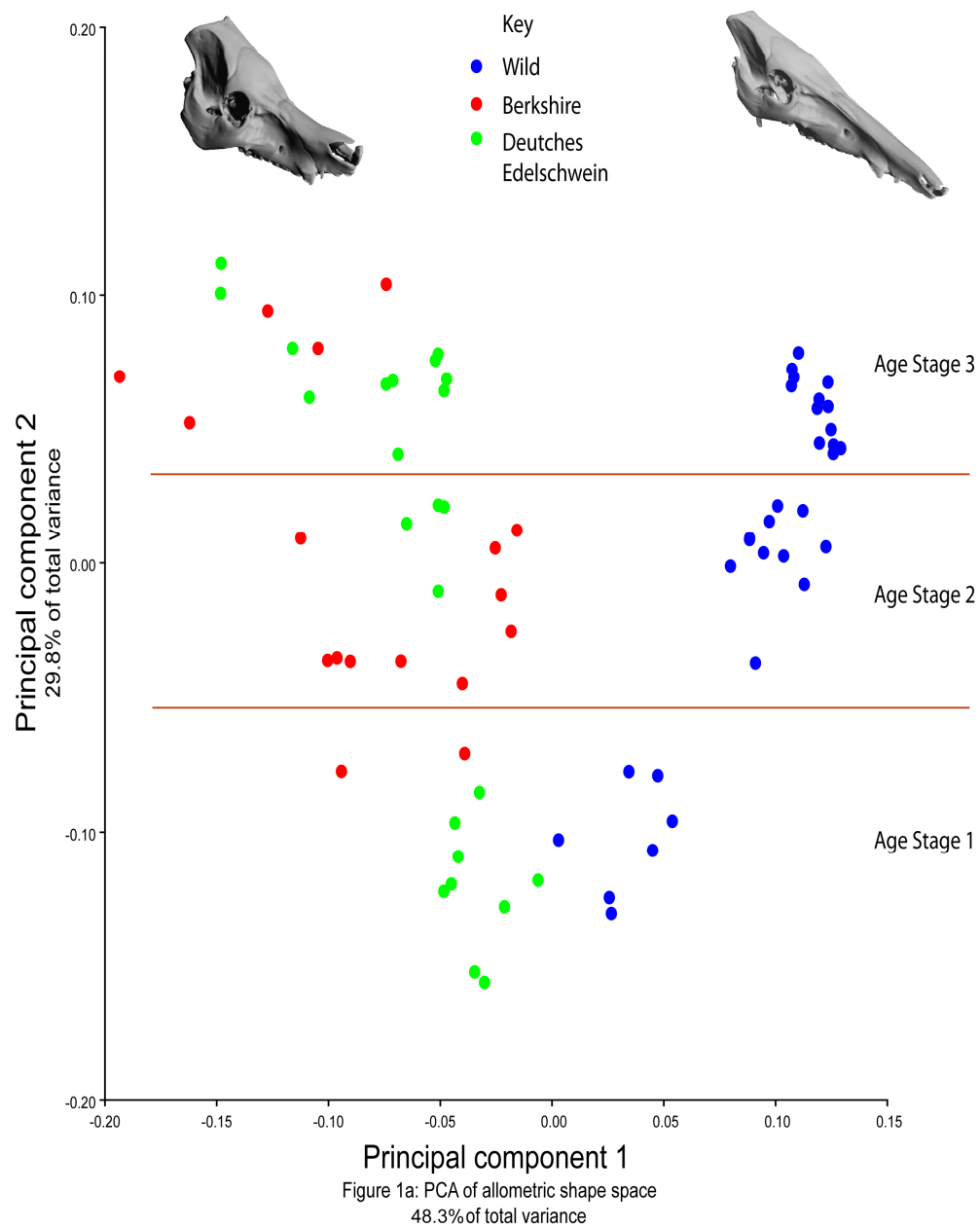
368 **Bibliography**

- 369 ALBARELLA, U., DOBNEY, K., ERVYNCK, A. & ROWLEY-CONWY, P. 2007.
 370 Introduction. In: ALBARELLA, U., DOBNEY, K., ERVYNCK, A. &
 371 ROWLEY-CONWY, P. (eds.) *Pigs and Humans: 10,000 Years of*
 372 *Interaction*. Oxford: Oxford University Press.
- 373 ALBERCH, P., GOULD, S. J., OSTER, G. F. & WAKE, D. B. 1979. Size and Shape
 374 in Ontogeny and Phylogeny. *Paleobiology*, 5, 296-317.
- 375 ARBUCKLE, B. S. 2005. *Experimental Animal Domestication and its Application to*
 376 *the Study of Animal Exploitation in Prehistory*, Oxford, Oxbow Books.
- 377 BELYAEV, D. K. 1979. Destabilizing Selection as a Factor in Domestication.
 378 *Journal of Heredity*, 70, 301-308.
- 379 BLANCO, M. B. & GODFREY, L. R. 2006. Craniofacial sexual dimorphism in
 380 *Alouatta palliata*, the mantled howling monkey. *Journal of Zoology*, 270,
 381 268-276.
- 382 BOKONYI, S. 1974. *History of Domestic Mammals in Central and Eastern Europe*,
 383 Budapest, Akademiai Kiado.
- 384 BOOKSTEIN, F. L. 1991. *Morphometric tools for landmark data: geometry and*
 385 *biology*, New York, Cambridge University Press.
- 386 COPPINGER, R., GLENDINNING, J., TOROP, E., MATTHAY, C.,
 387 SUTHERLAND, M. & SMITH, C. 1987. Degree of Behavioral Neoteny
 388 Differentiates Canid Polymorphs. *Ethology*, 75, 89-108.
- 389 CUCCHI, T., HULME-BEAMAN, A., YUAN, J. & DOBNEY, K. 2011. Early
 390 Neolithic pig domestication at Jiahu, Henan Province, China: clues from
 391 molar shape analyses using geometric morphometric approaches. *Journal of*
 392 *Archaeological Science*, 38, 11-22.
- 393 DAVID, B. 1990. Mosaic pattern of heterochronies: variation and diversity in
 394 Pourtalesiidae (deep-sea echinoids). *Evolutionary Biology*, 24, 297-327.
- 395 DRAKE, A. G. 2011. Dispelling dog dogma: an investigation of heterochrony in
 396 dogs using 3D geometric morphometric analysis of skull shape. *Evolution &*
 397 *Development*, 13, 204-213.
- 398 ERVYNCK, A., DOBNEY, K., HONGO, H. & MEADOW, R. 2001. Born Free?
 399 New Evidence for the Status of *Sus scrofa* at Neolithic Çayönü Tepesi
 400 (Southeastern Anatolia, Turkey). *Paléorient* 27, 47-73.
- 401 FANG, M., LARSON, G., RIBEIRO, H. S., LI, N. & ANDERSSON, L. 2009.
 402 Contrasting Mode of Evolution at a Coat Color Locus in Wild and Domestic
 403 Pigs. *Plos Genetics*, 5.
- 404 GODFREY, L. R. & SUTHERLAND, M. R. 1995. What's growth got to do with it -
 405 process and product in the evolution of ontogeny. *Journal of Human*
 406 *Evolution*, 29, 405-431.
- 407 GOULD, S. J. 1977. *Ontogeny and Phylogeny*, Cambridge MA, The Belknap Press
 408 of Harvard University Press.
- 409 GROVES, C. 1981. *Ancestors for the Pigs: Taxonomy and Phylogeny of the Genus*
 410 *Sus*, Canberra, Research School of Pacific Studies, Australian National
 411 University.
- 412 GRUBB, P. 2005. Order Artiodactyla. In: WILSON, D. E. & REEDER, D. M. (eds.)
 413 *Mammal Species of the World: a Taxonomic and Geographic Reference*. 3rd
 414 ed. Washington DC: Smithsonian Institution Press.
- 415 HARE, B., WOBBER, V. & WRANGHAM, R. 2012. The self-domestication
 416 hypothesis: evolution of bonobo psychology is due to selection against
 417 aggression. *Animal Behaviour*, 83, 573-585.

- 418 HIGHAM, C. F. W. 1967. Stock Rearing as a Cultural Factor in Prehistoric Europe.
419 *Proceedings of the Prehistoric Society*, 33, 84-106.
- 420 KLINGENBERG, C. P. 2008. *Morphoj* [Online]. University of Manchester, UK.:
421 Faculty of Life Sciences. Available:
422 http://www.flywings.org.uk/MorphoJ_page.htm.
- 423 LARSON, G., CUCCHI, T., FUJITA, M., MATISOO-SMITH, E., ROBINS, J.,
424 ANDERSON, A., ROLETT, B., SPRIGGS, M., DOLMAN, G., KIM, T. H.,
425 THUY, N. T. D., RANDI, E., DOHERTY, M., DUE, R. A., BOLLT, R.,
426 DJUBIANTONO, T., GRIFFIN, B., INTOH, M., KEANE, E., KIRCH, P.,
427 LI, K. T., MORWOOD, M., PEDRINA, L. M., PIPER, P. J., RABETT, R. J.,
428 SHOOTER, P., VAN DEN BERGH, G., WEST, E., WICKLER, S., YUAN,
429 J., COOPER, A. & DOBNEY, K. 2007. Phylogeny and ancient DNA of *Sus*
430 provides insights into neolithic expansion in island southeast Asia and
431 Oceania. *Proceedings of the National Academy of Sciences of the United*
432 *States of America*, 104, 4834-4839.
- 433 LARSON, G., DOBNEY, K., ALBARELLA, U., FANG, M. Y., MATISOO-
434 SMITH, E., ROBINS, J., LOWDEN, S., FINLAYSON, H., BRAND, T.,
435 WILLERSLEV, E., ROWLEY-CONWY, P., ANDERSSON, L. & COOPER,
436 A. 2005a. Worldwide phylogeography of wild boar reveals multiple centers
437 of pig domestication. *Science*, 307, 1618-1621.
- 438 LARSON, G., DOBNEY, K., ALBARELLA, U., MATISOO-SMITH, E., ROBINS,
439 J., LOWDEN, S., ROWLEY-CONWY, P., ANDERSSON, L. & COOPER,
440 A. 2005b. Domesticated pigs in eastern Indonesia - Response. *Science*, 309,
441 381-381.
- 442 MCKINNEY, M. L. & MCNAMARA, K. 1991. *Heterochrony: The Evolution of*
443 *Ontogeny*, New York, Plenum Press.
- 444 MITTEROECKER, P. & BOOKSTEIN, F. 2007. The conceptual and statistical
445 relationship between modularity and morphological integration. *Systematic*
446 *Biology*, 56, 818-836.
- 447 MITTEROECKER, P. & BOOKSTEIN, F. 2008. The evolutionary role of
448 modularity and integration in the hominoid cranium. *Evolution*, 62, 943-958.
- 449 MITTEROECKER, P. & GUNZ, P. 2009. Advances in Geometric Morphometrics.
450 *Evolutionary Biology*, 36, 235-247.
- 451 MITTEROECKER, P., GUNZ, P., BERNHARD, M., SCHAEFER, K. &
452 BOOKSTEIN, F. L. 2004. Comparison of cranial ontogenetic trajectories
453 among great apes and humans. *Journal of Human Evolution*, 46, 679-698.
- 454 MITTEROECKER, P., GUNZ, P. & BOOKSTEIN, F. L. 2005. Heterochrony and
455 geometric morphometrics: a comparison of cranial growth in *Pan paniscus*
456 versus *Pan troglodytes*. *Evolution & Development*, 7, 244-258.
- 457 MORAY, D. F. 1992. Size, shape, and development in the evolution of the domestic
458 dog. *Journal of Archaeological Science*, 19, 181-204.
- 459 MORAY, D. F. 1994. The early evolution of the domestic dog. *American Scientist*,
460 82, 336-347.
- 461 O'HIGGINS, P. & JONES, N. 1998. Facial growth in *Cercocebus torquatus*: an
462 application of three-dimensional geometric morphometric techniques to the
463 study of morphological variation. *Journal of Anatomy*, 193, 251-272.
- 464 O'HIGGINS, P. & JONES, N. 2006. *Tools for statistical shape analysis* [Online].
465 Hull York Medical School. Available:
466 <http://sites.google.com/site/hymsfme/resources>.

- 467 PRICE, E. O. 1999. Behavioral development in animals undergoing domestication.
 468 *Applied Animal Behaviour Science*, 65, 245-271.
- 469 ROHLF, F. J. 2003. Bias and error in estimates of mean shape in geometric
 470 morphometrics. *Journal of Human Evolution*, 44, 665–683.
- 471 TRUT, L. N. 1999. Early canid domestication: The farm-fox experiment. *American*
 472 *Scientist*, 87, 160-169.
- 473 TRUT, L. N., OSKINA, I. & KHARLAMOVA, A. 2009. Animal evolution during
 474 domestication: the domesticated fox as a model. *Bioessays*, 31, 349–360.
- 475 VIÐARSDÓTTIR, U. S., O'HIGGINS, P. & STRINGER, C. 2002. A geometric
 476 morphometric study of regional differences in the ontogeny of the modern
 477 human facial skeleton. *Journal of Anatomy*, 201, 211-229.
- 478 VIÐARSDÓTTIR, U. S. & COBB, S. 2004. Inter- and intra-specific variation in the
 479 ontogeny of the hominoid facial skeleton: testing assumptions of ontogenetic
 480 variability. *Annals of Anatomy* 186, 423-428.
- 481 ZEDER, M. 2012. Pathways to Animal Domestication. In: GEPTS, P., FAMULA, T.
 482 R., BETTINGER, R. L., BRUSH, S. B., DAMANIA, A. B., MCGUIRE, P.
 483 E. & QUALSET, C. O. (eds.) *Biodiversity in Agriculture: Domestication,*
 484 *Evolution, and Sustainability*. Cambridge: Cambridge University Press.
- 485 ZEDER, M. A. 2008. Domestication and early agriculture in the Mediterranean
 486 Basin: Origins, diffusion, and impact. *Proceedings of the National Academy*
 487 *of Sciences*, 105, 11597-11604.
- 488

489
 490 **Figure 1:** PCA showing first two PCs of wild and domestic ontogenetic series. The
 491 two domestic series are on the left (negative score on PC1), and the wild series on the
 492 right (positive score on PC1). PC2 shows accruing size and age, and the increasing
 493 distance between the wild and domestic ontogenetic series. No discrimination was
 494 discernible on other PCs.



495

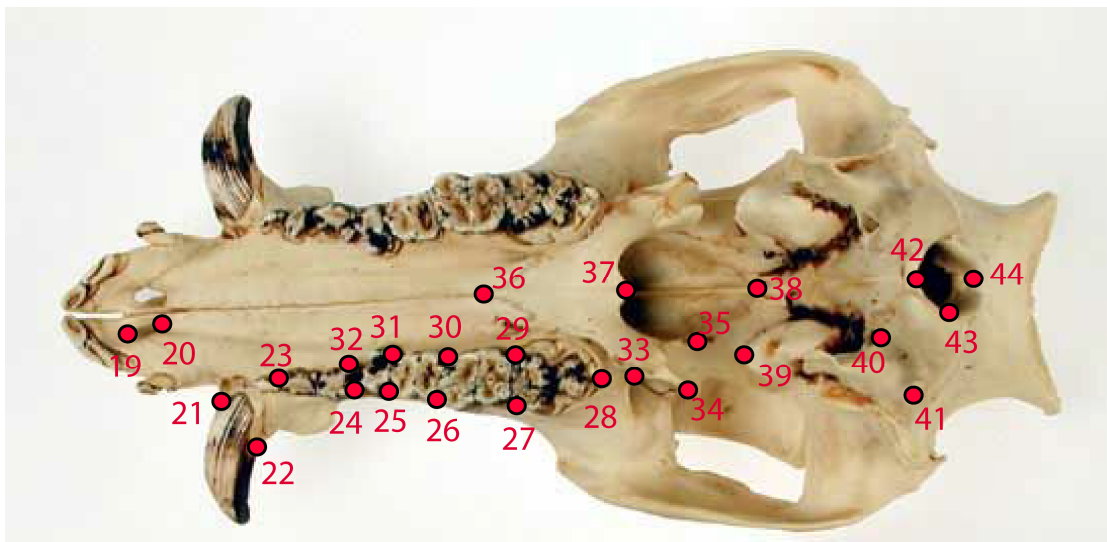
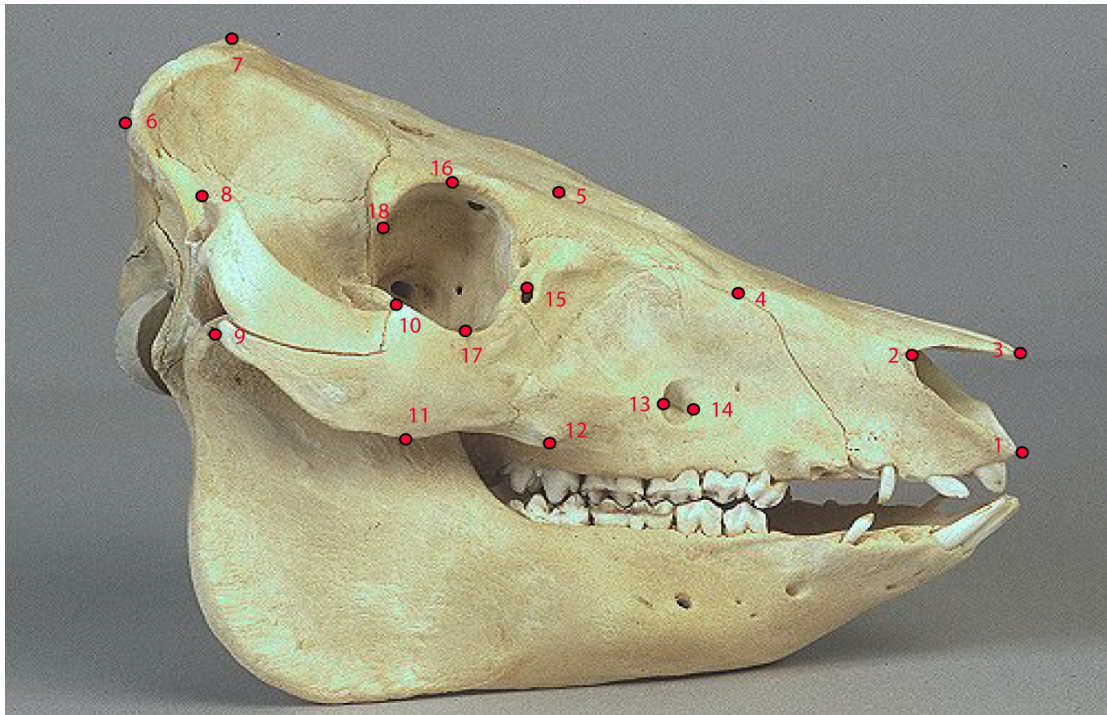
Table S1:Landmark List

Landmark	Description
1	Most anterior midline point on nasals.
2	Anterior join in nasal and pre maxilliar suture.
3	Anterior point of nasal.
4	Suture at the meeting point of the premaxillar, maxillar and nasal.
5	Most posterior point of superorbital foramen and groove.
6	Most lateral point of the Nuchal Crest.
7	Most anterior point of Nuchal Crest - on the midline of the parietal.
8	Most superior point of zygomatic process of temporal.
9	Most posterior point of zygomatic process of malar.
10	Superior point of the temporal process of malar.
11	Most inferior point of the malar (zygomatic arch).
12	Anterior most point of the process emerging of the malar (zygomatic arch).
13	Most posterior point of infraorbital foramen.
14	Most anterior point of infraorbital foramen.
15	Most superior point of the lower lacrimal foramina.
16	Most superior point of the occipital.
17	Most inferior point of the occipital.
18	Base of supraorbital process.
19	Anterior point of incisive foramen/palatine fissure.
20	Posteriormost point of incisive foramen/palatine fissure.
21	Most anterior point of canine alveolus.
22	Most posterior point of canine alveolus.
23	Anterior point of the alveolar margin of the tooth row.
24-27	Contact points between M3/M2, projected labially (buccally) onto alveolar margin.
28	Most posterior point of the alveolar margin of the tooth row.

- 29-32 Contact points between M3/M2, projected lingually onto alveolar margin.
- 33 Most anterior point of the pterygoid process of the palatine.
- 34 Most lateral point of the pterygoid process of the palatine.
- 35 Most posterior point of the pterygoid process of the palatine.
- 36 Suture of the nasal and palatine bones (on the midline).
- 37 Tip of posterior nasal spine.
- 38 Meeting point between the basisphenoid and basioccipital along midline, posterior of the vomer.
- 39 Anterior most point of the bulla tympanica.
- 40 Most anterior point of the paramastoid process.
- 41 Most anterior point on the margin of the Hypoglossal canal.
- 42 Lowest point on the orobasal border of foramen magnum.
- 43 Most posterior tip of occipital condyle.
- 44 Most superior point on the border of foramen magnum.

Table S2: Subsets of landmarks (Paper 3/Chapter 5)

Landmarks	Region
Parietal	4,5,6,7,44
Zygomatic	8,9,10,11,12
Angle of the	2,3,4,5,6,44
Nasal	
Orbit	15,16,17,18
Toothrow	21-32
Basicranium	33-41



Supporting Table S2

	S.s. Tunis	S.s. Berlin	S.s. Caucasus	S.s.Fukien	S.s.Szechuan	S.s.Hainan	S.s.Shanxi	S.s.Gansu	S.s. E.Poland
S.s. Tunis	60.0								
S.s. Berlin		46.9	3.1	3.1					9.4
S.s. Caucasus			60.0		5.0				5.0
S.s.Fukien			61.5	15.4	7.7				
S.s.Szechuan			1.0	30.0	30.0				
S.s.Hainan				66.6	33.3	0.0			
S.s.Shanxi							57.1	14.3	14.3
S.s.Gansu					25.0		25.0	25.0	
S.s. E.Poland		10.7	3.6						67.9
S.s.Geneva		6.1							6.1
S.s. Iraq/Iran			11.1	11.1					
S.s N.E.Iran			14.3						
S.s S.Iran		20.0							
S.s. Turkey	37.5		12.5						
S.s. S.W.Germany		7.7							
S.s. S.W.Poland		12.5	6.3						31.3
S.s.Burma					15.4				
S.s India			5.6	11.1			5.6		
S.s Japan									
S.s Malaysia					14.3	14.3			
S.s Papua				11.1					
S.s Sardinia									
S.s N.Sumatra									
S.s. Ligga Is									
S.s. Nias IS									
S.s W.Russia		16.7	33.3						

Supporting Table S2

S.s.Geneva	S.s. Iraq/Iran	S.s N.E.Iran	S.s S.Iran	S.s. Turkey	S.s. S.W.Germany	S.s. S.W.Poland	S.s.Burma	S.s India	S.s Japan	S.s Malaysia
10.0				30.0						
6.3					6.3	9.4				
				15.0	5.0			10.0		
							7.7	7.7		
							30.0			
								14.3		
							25.0			
3.6						14.3				
72.7				6.1	3.0					
	55.6	11.1	11.1							
		42.9	28.6			14.3				
		60.0	20.0							
				37.5						
23.1				7.7	53.8	7.7				
6.3						37.5				
							53.8	7.7		15.4
	5.6					5.6	5.6	55.6		
									100.0	
							14.3			57.1
							4.3	4.3		
16.7				16.7						

Supporting Table S2

S.s Papua	S.s Sardinia	S.s N.Sumatra	S.s. Ligga Is	S.s. Nias IS	S.s W.Russia
		3.1	3.1		9.4
					6.1
					12.5
	6.3	7.7	5.6		
89.9	100.0	91.3			
		57.1	42.9		
			40.0	60.0	
					16.7

7 Conclusion

This thesis comprised of four main research questions, conducted through the methodology of geometric morphometrics to answer questions about pig evolution (manuscript 1), to study in greater depth suid biogeographic variation (manuscript 2), to quantify differences between wild and domestic *Sus scrofa* (manuscript 3), and to investigate the effects of heterochrony on domestic pigs (manuscript 4). The results are summarised here, along with the implications of the results and some possible avenues of future research.

7.1 Evolutionary studies in suids (manuscript 1)

The relationship between the African suid *Potamochoerus* and the Eurasian suid *Sus* was investigated by combining shape analysis of modern material with evolutionary depth of genetic analysis. This answered a long standing question about the relationship between these two genera. Their morphological similarity had been noted for some time (Groves, 1981), but this appeared to be contradicted by the monophyly of African Suids as confirmed through genetic analysis (Gongora et al., 2011). The mechanism that could have brought this about was not known, only postulated. The results of manuscript 1 showed that the genetic analysis revealing African and Eurasian suids to be monophyletic was not incongruous with morphology, as suid morphology is explained by suid cranial shape reflecting signatures derived from its evolutionary and behavioural ancestry. Thus the genetic and morphological variation within suids reveals an important component of the evolutionary history of the family Suidae, a complete understanding of which can only be achieved through an analysis of both.

The approaches employed in this study, especially the combination of morphology and genetics, could be used to resolve a range of similar issues in other taxonomic groups, such as the Family Rhinocerotidae (Willerslev et al., 2009) and the tribe Papionini (Gilbert, 2011).

7.2 Biogeographic variation in suids (manuscript 2)

Sus scrofa is a species that shows strong biogeographic structuring, both in its morphology and genetics reflecting its large range throughout Eurasia and North Africa. A GMM approach returned a detailed resolution of the biogeography of *Sus*,

confirming that this approach has great scope for use in biogeographic studies as has also been shown in African monkeys (Cardini et al., 2007, Cardini and Elton, 2009). This is important implications where subspecies have been ascribed largely on the basis of cranial characteristics (Groves, 1981, 2007, Genov, 1999), which often rely on order of magnitude measurements. Our results have shown that size is more affected than shape by climate, which could impact taxonomic studies. A combined genetic and morphometric approach may prove to be the most informative approach in the future.

This result is also significant with regard to studies of determination of status as wild or domestic, these too are mainly based on size differences (Payne and Bull, 1988, Mayer et al., 1998). These investigations are based on the assumption that wild and domestic individuals are morphologically different from each other and that this difference is significant, be it in cranial characteristics, tooth size or overall body size. However, these characteristics are strongly affected by climate, diet, habitat and geography, making the individuals a product of their surroundings. Studies investigating domestic status of suids must therefore take into account possible dietary changes or environmental shifts. This will mainly affect regional or wide temporal studies which should include baseline comparisons with wild animals and other domestics to check for possible climatic shifts.

7.3 Discrimination between wild and domestic suid morphology (manuscript 3)

It is possible to discriminate between wild and domestic pigs on the basis of cranial morphology. This is true for both whole and partial crania such as the parietal, zygomatic, angle of the nasal and the basicranium. The ability to determine between different morphologies, either in cranial or post cranial material has significant implications for zooarchaeology. Greater resolution allows clearer quantification of the proportion of wild and domestic animals on a site, elucidating evolving subsistence strategies and could help determine the origins of the transition from hunter-gathering to farming (Rowley-Conwy et al., 2012).

The sensitivity of GMM allows for the distinction between domestic breeds. Currently the study of the history of breeds is focused around the industrial revolution, but there is tentative evidence in the archaeological record of distinct

breeds before this period (Davis, 2008, Davis et al., 2012). This has important consequences for the study of the origins and development of such breeds, where currently the methodology for studying improvement is based on size increases (Davis et al., 2012), which has obvious difficulties overcoming size issues associated with sexual dimorphism. Breed improvement, for traction or increased meat bearing should be reflected in the morphology, not just size, and could be examined using the methods employed here without being confused with the effects of sexual dimorphism.

The results of this paper demonstrate some of the possible applications for GMM in archaeology. Studies have already started applying GMM to zooarchaeological questions and material, for example shape differences have been shown to exist between wild and domestic pig teeth in the early archaeological record, and GMM can discriminate between human populations on the basis of mandibular morphology (Buck and Vidarsdottir, 2004). GMM can be applied to post-cranial material as well, e.g. it has been applied to both Palaeolithic horse metapodials to investigate phylogeography (Bignon et al., 2005) and cervid anatomy associated with locomotion for palaeo-climatic reconstruction of the Plio-Pleistocene (Curran, 2012). There is great scope for future applications on cranial and post-cranial material, not just to elucidate both the process and history of domestication, but any archaeological question that requires discrimination between populations, or wishes to examine morphological change or evolution.

7.4 Domestication and Heterochrony in *Sus scrofa* (manuscript 4)

In the archaeological literature of domestication, heterochrony is still evoked as the causal mechanism of morphological change, with domestic animals typed as paedomorphic wild animals (Zeder, 2012, Hare et al., 2012). Although some paedomorphic behavioural characters in domestic animals have been identified (Coppinger et al., 1987, Moray, 1992, Moray, 1994, Trut et al., 2009), morphological characters classified as paedomorphic cannot be quantified in either domestic pigs or dogs. Thus heterochrony is not the cause of the domestic phenotype, nor are most domestic pigs paedomorphic.

Clearly there is some pre- or post-natal mechanism or process that is enforcing changes to morphology, yet the traditional language of heterochrony appears inadequate to explain it. We must also keep in mind that the processes acting prenatally may not be the same as those acting postnatally.

If heterochrony is not the causal mechanism for morphological change in domestic animals then there is currently no explanation for why the domestic phenotype exists in many varied and different species. Further definition of the changes that occur during growth and development may help answer this question. Analysis of other domesticates, like horses, sheep or cattle may show commonalities in the development of domestication. There are experiments that manipulate the conditions of growth in domestic animals e.g. the fox farm experiment by Belyaev (Belyaev, 1979, Trut, 1999) or various experiments on mice or rats (Arbuckle, 2005). Multivariate analysis of the crania of the specimens in those experiments would allow specific links to be drawn between morphological development, hormone fluctuation and the genetic mechanisms behind them.

7.5 Strengths, weaknesses and recommendations for future work.

A weakness in this study is the lack of complete geographic coverage for the biogeographic study (Manuscript 2). Adequate samples were not available for the Iberian peninsular, south east Europe, central and eastern Russia, central Asia and especially North Africa. The paucity of North African material is a more widespread problem with suid studies as there are not many samples in museum collections (Groves, 1981), their relationship with Near Eastern and European pigs is not fully understood (Groves, 1981, Larson et al., 2005). Future work would ideally fill in these gaps, and attempt to resolve the relationships of pigs in the western Mediterranean Basin, central Asia and North Africa. Future studies of taxonomy could use a combined GMM and genetics approach, which would resolve the morphology and genetics to produce a confident, comprehensive taxonomy for pigs.

A lack of data is also hindering the study of domestic suid ontogeny; with only two and half complete ontogenetic series the results are tentative, although even with a limited amount of data we nearly returned a significant result. With more data this study would be considerably strengthened. This study also presents one of the major

avenues for future research. Studies of domestication are of increasing importance as they have become recognised as studies of evolution (Zeder, 2006, Zeder et al., 2006a). GMM is appreciably more powerful and flexible than traditional biometrical approaches, which combined with genetics and hormone studies could produce major breakthroughs in this field.

GMM as a tool is only just starting to find applications within the field of archaeology. As this thesis demonstrates GMM is an excellent at discriminating between populations and also tracing and explaining evolutionary patterns. It can be directly integrated with the other major innovative field of current archaeology, genetics (Zeder et al., 2006b) in a way that traditional methods have not (Davis et al., 2012), and perhaps may struggle to. Overall this thesis has used GMM as a tool in biological and archaeological contexts, demonstrating its ability to answer varied and complex questions. Hopefully applications of GMM in these contexts will continue, as I firmly believe that GMM has the ability to provide more detail to standing archaeological questions, and help explain the evolution of human society.

Bibliography

- ARBUCKLE, B. S. 2005. *Experimental Animal Domestication and its Application to the Study of Animal Exploitation in Prehistory*, Oxford, Oxbow Books.
- BELYAEV, D. K. 1979. Destabilizing Selection As A Factor In Domestication. *Journal of Heredity*, 70, 301-308.
- BIGNON, O., BAYLAC, M., VIGNE, J. D. & EISENMANN, W. 2005. Geometric morphometrics and the population diversity of Late Glacial horses in Western Europe (*Equus caballus arcelini*): phylogeographic and anthropological implications. *Journal of Archaeological Science*, 32, 375-391.
- BUCK, T. J. & VIDARSDOTTIR, U. S. 2004. A proposed method for the identification of race in sub-adult skeletons: A geometric morphometric analysis of mandibular morphology. *Journal of Forensic Sciences*, 49, 1159-1164.
- CARDINI, A. & ELTON, S. 2009. Geographical and taxonomic influences on cranial variation in red colobus monkeys (Primates, Colobinae): introducing a new approach to 'morph' monkeys. *Global Ecology and Biogeography*, 18, 248-263.
- CARDINI, A., JANSSON, A. U. & ELTON, S. 2007. A geometric morphometric approach to the study of ecogeographical and clinal variation in vervet monkeys. *Journal of Biogeography*, 34, 1663-1678.
- COPPINGER, R., GLENDINNING, J., TOROP, E., MATTHAY, C., SUTHERLAND, M. & SMITH, C. 1987. Degree of Behavioral Neoteny Differentiates Canid Polymorphs. *Ethology*, 75, 89-108.

- CURRAN, S. C. 2012. Expanding ecomorphological methods: geometric morphometric analysis of Cervidae post-crania. *Journal of Archaeological Science*, 39, 1172-1182.
- DAVIS, S. J. M. 2008. Zooarchaeological evidence for Moslem and Christian improvements of sheep and cattle in Portugal. *Journal of Archaeological Science*, 35, 991-1010.
- DAVIS, S. J. M., SVENSSON, E. M., ALBARELLA, U., DETRY, C., GOTHERSTROM, A., PIRES, A. E. & GINJA, C. 2012. Molecular and osteometric sexing of cattle metacarpals: a case study from 15th century AD Beja, Portugal. *Journal of Archaeological Science*, 29, 1445-1454.
- GENOV, P. V. 1999. A Review of the Cranial Characteristics of the Wild Boar (*Sus scrofa* Linnaeus 1758), with Systematic Conclusions. *Mammal Review*, 29, 205-238.
- GILBERT, C. C. 2011. Phylogenetic analysis of the African papionin basicranium using 3-D geometric morphometrics: The need for improved methods to account for allometric effects. *American Journal of Physical Anthropology*, 144, 60-71.
- GONGORA, J., CUDDAHEE, R. E., NASCIMENTO, F. F. D., PALGRAVE, C. J., LOWDEN, S., HO, S. Y. W., SIMOND, D., DAMAYANTI, C. S., WHITE, D. J., TAY, W. T., RANDI, E., KLINGEL, H., RODRIGUES-ZARATE, C. J., ALLEN, K., MORAN, C. & LARSON, G. 2011. Rethinking the evolution of extant sub-Saharan African suids (Suidae, Artiodactyla). *Zoologica Scripta*, 40, 327-335.
- GROVES, C. 1981. *Ancestors for the Pigs: Taxonomy and Phylogeny of the Genus Sus*, Canberra, Research School of Pacific Studies, Australian National University.
- GROVES, C. 2007. Current views on taxonomy and zoogeography of the genus *Sus*. In: ALBARELLA, U., DOBNEY, K. & ROWLEY-CONWY, P. (eds.) *Pigs and Humans: 10,000 years of interaction*. Oxford: Oxford University Press.
- HARE, B., WOBBER, V. & WRANGHAM, R. 2012. The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour*, 83, 573-585.
- LARSON, G., DOBNEY, K., ALBARELLA, U., FANG, M. Y., MATISOO-SMITH, E., ROBINS, J., LOWDEN, S., FINLAYSON, H., BRAND, T., WILLERSLEV, E., ROWLEY-CONWY, P., ANDERSSON, L. & COOPER, A. 2005. Worldwide phylogeography of wild boar reveals multiple centers of pig domestication. *Science*, 307, 1618-1621.
- MAYER, J. J., NOVAK, J. M. & BRISBIN JR., I. L. 1998. Evaluation of Molar Size as a Basis for distinguishing Wild Boar from Domestic Swine: Employing the Present to Decipher the Past. In: NELSON, S. M. (ed.) *Ancestors for the Pigs: Pigs in Prehistory*. Philadelphia: Museum Applied Science Centre for Archaeology.
- MORAY, D. F. 1992. Size, shape, and development in the evolution of the domestic dog. *Journal of Archaeological Science*, 19, 181-204.
- MORAY, D. F. 1994. The early evolution of the domestic dog. *American Scientist*, 82, 336-347.
- PAYNE, S. & BULL, G. 1988. Components of variation in measurements of pig bones and teeth, and the use of measurements to distinguish wild from domestic pig remains. *ArchaeoZoologia*, 2, 27-65.

- ROWLEY-CONWY, P., ALBARELLA, U. & DOBNEY, K. 2012. Distinguishing Wild Boar from Domestic Pigs in Prehistory: A Review of Approaches and Recent Results. *Journal of World Prehistory*, 25, 1-44.
- TRUT, L. N. 1999. Early canid domestication: The farm-fox experiment. *American Scientist*, 87, 160-169.
- TRUT, L. N., OSKINA, I. & KHARLAMOVA, A. 2009. Animal evolution during domestication: the domesticated fox as a model. *Bioessays*, 31, 349–360.
- WILLERSLEV, E., GILBERT, M. T. P., BINLADEN, J., HO, S. Y. W., CAMPOS, P. F., RATAN, A., TOMSHO, L. P., DA FONSECA, R. R., SHER, A., KUZNETSOVA, T. V., NOWAK-KEMP, M., ROTH, T. L., MILLER, W. & SCHUSTER, S. C. 2009. Analysis of complete mitochondrial genomes from extinct and extant rhinoceroses reveals lack of phylogenetic resolution. *Bmc Evolutionary Biology*, 9.
- ZEDER, M. 2012. Pathways to Animal Domestication. In: GEPTS, P., FAMULA, T. R., BETTINGER, R. L., BRUSH, S. B., DAMANIA, A. B., MCGUIRE, P. E. & QUALSET, C. O. (eds.) *Biodiversity in Agriculture: Domestication, Evolution, and Sustainability*. Cambridge: Cambridge University Press.
- ZEDER, M. A. 2006. Central Questions in the Domestication of Plants and Animals. *Evolutionary Anthropology*, 15, 105-117.
- ZEDER, M. A., BRADLEY, D. G., EMSHWILLER, E. & SMITH, B. D. 2006a. Documenting Domestication Bringing Together Plants, Animals, Archaeology, and Genetics. In: ZEDER, M. A., G., B. D., E., E. & D., S. B. (eds.) *Documenting Domestication: New Genetic and Archaeological Paradigms*. Berkeley, Los Angeles, London: University of California Press.
- ZEDER, M. A., EMSHWILLER, E., SMITH, B. D. & BRADLEY, D. G. 2006b. Documenting domestication: the intersection of genetics and archaeology. *Trends in Genetics*, 22, 139-155.